43335

National Library of Canada | Bibliothèque nationale du Canada

CANADIAN THESES ON MICROFICHE | THÈSES CANADIENNES SUR MICROFICHE

NAME OF AUTHOR/*NOM DE L'AUTEUR* Audrey Dianne Balfour

TITLE OF THESIS/*TITRE DE LA THÈSE* Micro-Image Stimulation as a Behavioral Profiling Technique in Columbian Ground Squirrels

UNIVERSITY/*UNIVERSITÉ* University of Alberta

DEGREE FOR WHICH THESIS WAS PRESENTED/*GRADE POUR LEQUEL CETTE THÈSE FUT PRÉSENTÉE* M. Sc.

YEAR THIS DEGREE CONFERRED/*ANNÉE D'OBTENTION DE CE GRADE* 1979

NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* Dr. André Steiner

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

DATED/*DATÉ* June 6, 1979 SIGNED/*SIGNÉ* A. Diane Balfour

PERMANENT ADDRESS/*RÉSIDENCE FIXÉ* # 11 358 Erb St.
Waterloo, Ontario

NL-91 (3-74)

National Library of Canada

Cataloguing Branch
Canadian Theses Division

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada

Direction du catalogage
Division des thèses canadiennes

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

THE UNIVERSITY OF ALBERTA

Mirror-Image Stimulation as a Behavioral Profiling Technique in Columbian Ground Squirrels

by

© A.D. Balfour

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Department of Zoology

EDMONTON, ALBERTA

Fall, 1979

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Mirror-Image Stimulation as a Behavioral Profiling Technique in Columbian Ground Squirrels submitted by A.D. Balfour in partial fulfilment of the requirements for the degree of Master of Science.

.....

Supervisor

.....

.....

.....

.....

Date.....April 23rd 1979.....

Abstract

Mirror-image stimulation (MIS) was used to determine behavioral profiles in Columbian ground squirrels. Behaviors observed during MIS were significantly different from those observed in the same apparatus with the mirror covered and were consistent with the contention that a mirror-image is viewed as an unfamiliar conspecific . Multivariate classification procedures reduced MIS-derived profiles to three statistically distinct "types" characterized as "Sociable", "Avoider", and "Conflict". Changes of MIS type upon retesting were rare, suggesting that whatever MIS measures is relatively stable.

The proportions of MIS types did not differ significantly between sex and age classes, but did vary with socioecological situation. Sociable animals were most likely to live in colonies, whereas Conflict animals tended to live either in shrub or satellite situations. Avoiders were relatively evenly distributed over the three situations.

Field observations of behavior were made for 15 adult females that were also exposed to MIS. Analysis indicated significant differences between behavioral types for a number of activity and social interaction variables. It is suggested that MIS reveals fundamental behavioral differences which may be important in ground squirrel social structure and population dynamics.

Acknowledgements

I would like to thank Dr. André Steiner for his supervision and support. Drs. Jan Murie and Fred Zwickel also provided helpful suggestions and critical comments. Andy Wroot, Connie Griffiths, C. Grobben, and the Educational Research Services staff advised on the various statistical analyses. Dan Precht, Ray Weingardt, and Andy Wroot helped with many computer problems. Catherine Storey and Hazel Speed provided field assistance.

Financial support was supplied by a National Research Council of Canada grant to Dr. André Steiner, and by the Department of Zoology at the University of Alberta. Studies were conducted on the property of Mr. Lyman Garner.

Finally, special thanks to Craig Hawryshyn for providing much needed psychological support and encouragement.

Table of Contents

Chapter		Page
I.	Introduction	1
II.	Mirror-Image Stimulation	5
III.	METHODS	10
	Trapping and Marking	12
	MIS Apparatus and Testing Procedure	12
	Experimental Animals	15
	Field Observations	18
IV.	MULVARIATE ANALYSIS OF MIS DATA	22
	R-Factor Analysis	24
	Results of R-Factor Analysis for the 10 Minute Period Before Mirror Exposure	27
	Results of R-Factor Analysis for the 10 Minute Period After Mirror Exposure	29
	Comparison of 10 Minute Periods Before and After Mirror Exposure	31
	Results of R-Factor Analysis for the Full 15 Minutes of MIS	36
	Description of Columbian Ground Squirrel Responses to MIS	39
V.	CLASSIFICATION OF INDIVIDUALS ON THE BASIS OF MIS RESPONSE	42
	Linear Typal Analysis	42
	Cluster Analysis	47
	Comparison of Classifications Obtained Using Linear Typal Analysis and Cluster Analysis	49
	Description of MIS-Derived Behavioral Types	53
	Discriminant Analysis	57

VI. CONSISTENCY OF MIS TYPES OVER TIME.....62

VII. THE DISTRIBUTION OF BEHAVIORAL TYPES: MULTIDIMENSIONAL CONTINGENCY TABLE ANALYSIS.....66

VIII. FIELD OBSERVATIONS OF MIS TYPES.....73

Differences Between Sampling Periods.....75

Differences Between Behavioral Types.....78

Home Range Size and Percent Overlap of Home Range.....81

MIS Types Within Litters.....82

IX. DISCUSSION.....84

Literature Cited.....95

Appendix 1.....100

Appendix 2a.....101

Appendix 2b.....102

Appendix 2c.....103

List of Tables

Table		Page
1	Densities of adult ground squirrels in open colonial and dense shrub situations	11
2	Behavioral categories recorded during MIS	14
3	Sex, age, and socioecological situation of animals used in repeat MIS tests	16
4	Sex, age, and socioecological situation of animals used in single MIS tests	17
5	Behavioral variables recorded during or calculated after focal animal sampling	19
6	Varimax rotated factor matrix based on 23 behaviors exhibited during the 10 minute period with the mirror covered	28
7	Varimax rotated factor matrix based on 23 behaviors exhibited during the 10 minute period with the mirror exposed	30
8	Correlations between factors representing behaviors before and after mirror exposure	32
9	Varimax rotated factor matrix based on 31 behaviors exhibited during MIS	37
10	Primary cosine matrix of the three pure types extracted from MIS data by linear typal analysis	46
11	Increases of error sum of squares at selected stages of the clustering process	50
12	Similarities between partitions: contingency tables comparing cluster and linear typal analysis classifications	54
13	Comparison of results using different classification procedures: number of animals in each class	55
14	Repeated measures analysis of variance based on first discriminant function scores	63

List of Tables - Continued

Table		Page
15	Repeated measures analysis of variance based on second discriminant function scores	64
16	Four-way contingency table showing MIS type as a function of age, sex, and socioecological situation	67
17	Selected models assuming various sets of interactions among the four variables tested against the observed data	68
18	Partitioning of likelihood ratio chi-square statistic: differences between tested models	70
19	Two-way contingency table comparing MIS type and socioecological situation	71
20	Breakdcwn of core group animals by MIS type and socioecological situation	74
21	Field observations: results of Hodges-Lehmann tests for differences between MIS types and sample periods	76
22	Behavioral types of satellite litters	83

List of Figures

Figure | Page

1 Mean profiles from the 10 minute periods before and after mirror exposure.....35

2 Linear typal analysis: pure type profiles.....45

3 Cluster analysis: profiles based on mean cluster scores.....52

4 Scatterplot of three MIS types against two discriminant functions.....61

I. Introduction

A particular social system is a product of the complex interaction of many factors: environmental conditions, population density, age/sex structure, kinship, and the use of space are perhaps the most commonly recognized and studied. Less frequently taken into account are those factors variously designated as "behavioral phenotypes" (Bekoff, 1977), "behavioral profiles" (Svendsen and Armitage,1973), and "behavioral types" (Krebs,1970). The fact that these terms are often used synonymously, and perhaps carelessly, should not negate their consideration. For the purposes of this paper, "behavioral phenotype" will refer to observable behavioral characteristics of the organism "as they have developed under the combined influences of the genetic constituents of the individual and the effect of environmental factors" (Wilson,1975). "Profile" will refer to a graphical representation of an individual's scores on a series of variables, specifically, that line connecting all adjacent score points (DuMas,1949). A "behavioral profile" may thus be used to describe the results of a particular test or the results of a series of observations. Finally, "behavioral type" will refer to a subgrouping of individuals with similar profiles. Behavioral profiles and behavioral types are thus products of attempts to measure the behavioral phenotypes of a given sample of individuals within a population.

An individual animal possesses a unique behavioral phenotype comprising its entire behavioral repertoire, including idiosyncratic behaviors as well as those associated with a particular age, sex, or social status. The variability of behavioral phenotypes within a population is best envisaged as a continuum and the imposition of a typology upon such a continuum may seem arbitrary and artificial. Typologies and classification schemes, however, are heuristic devices which may facilitate our comprehension of complex social systems. Whether recognized as such or not, typologies are ubiquitous in the behavioral literature and are, undoubtedly, both invaluable and unavoidable given the current state of the art.

The behavioral and ecological literature contains frequent suggestions that behavioral phenotypes or the proportions of behavioral types within a population may have important consequences for population regulation and social organization. Bekoff (1977) and Fairbairn (1978), for example, have pointed out that behavioral type may be an important factor in determining which individuals disperse. Krebs (1970) found that the proportions of behavioral types changed with fluctuations in population density. Fox (1975) reported that a variety of behavioral profiles occurred within canid litters and hypothesized that intralitter behavioral heterogeneity enhanced pack formation, while intralitter homogeneity promoted dispersal. Finally, there is the work by Svendsen and Armitage (1973) which provided

the model for the present study. Svendsen and Armitage used mirror-image stimulation (MIS) to determine individual behavioral profiles of marmots. Svendsen (1974) reported that these profiles, broadly classified as three types, affected social interactions, spatial distribution, and population dynamics of marmots.

Ground squirrels (Spermophilus spp.) share many of the characteristics of marmots which render them so appropriate for field studies of behavior. Both genera are diurnal, readily observable, and frequently live in groups or "colonies". I studied the Columbian ground squirrel, (Spermophilus columbianus), a species whose behavior has been previously described by Steiner (1970a, 1970b, 1971, 1972, 1973, 1974, 1975), Betts (1976), and Murie and Harris (1978). Different results and interpretations between these studies suggested the variability of social organization within the species. My fieldwork in southwestern Alberta indicated that Columbian ground squirrels, like marmots, live in a variety of social situations even within a limited area of relatively homogeneous habitat. Subsequent laboratory work on captive squirrels showed that their responses to MIS were very like those described for marmots by Svendsen and Armitage (1973).

Svendsen and Armitage (1973) suggested that MIS could provide behavioral profiles consistent with behavioral patterns observed in the field. They also reported that certain MIS-derived behavioral types tended to be more

frequent in particular social situations. Armitage (1975) later incorporated the concept of behavioral types into a general model relating social behavior to population dynamics in marmots. Given the similarities between marmots and Columbian ground squirrels in terms of responses to MIS, social organization, and ecological niche, it seemed that MIS might also prove a valuable tool for ground squirrel behavioral studies. To assess the potential of MIS as a behavioral profiling technique and an index of social behavior for Columbians, I sought to answer the following questions:

1. Do behavior patterns observed when the mirror is exposed differ from those observed in the identical apparatus when the mirror is covered?
2. Can individual profiles derived from MIS be classified into a smaller set of distinct behavioral types?
3. Does MIS give repeatable results over time?
4. If distinct behavioral types exist, are they evenly distributed among animals of different sexes, ages, and socioecological situations?
5. If distinct behavioral types exist, are these types distinguishable on the basis of their behaviors in the field?

II. Mirror-Image Stimulation

The term "mirror-image stimulation" was initially used by Gallup (1968) to describe the situation in which an animal is confronted by its mirror-image. Gallup(1968) reviewed previously reported vertebrate responses to mirrors and concluded that MIS could be a useful technique for studying animal social behavior. The utility of the technique depends upon the presence of adequately developed visual receptors and the extent to which the test animal responds to the mirror-image as if it were a conspecific.

The visual systems of sciurids have been examined extensively in recent years. These highly diurnal animals have one obvious adaptation which has provoked the interest of biologists: the predominance of cones in the retina (Jacobs, 1978). Studies on the electrophysiology (Michael, 1968, 1972, 1973) and anatomy of ground squirrel eyes (Vaidya, 1964; Tigges, 1970; West and Dowling, 1972) have been supplemented by behavioral investigations in several species (Jacobs, 1978). All research to date indicates that ground squirrels have color vision similar to that of a human dichromatic observer (Jacobs, 1978) The different ground squirrels examined so far (Mexican ground squirrel, Spermophilus mexicanus; thirteen-lined ground squirrel, Spermophilus tridecemlineatus; antelope ground squirrel, Ammospermophilus harrisi; and the related prairie dog, Cynomys ludovicianus) apparently all have both color vision and visual capacities which are unusually keen among

mammalian species in general and rodents, in particular (Jacobs, 1978). In the absence of specific information concerning vision in Columbian ground squirrels, it seems reasonable to assume that their visual system would be very like those of other species and would, therefore, be more than adequate to respond to a mirror-image and to see the imageas another squirrel.

Animals with adequate visual sensitivity typically respond to a mirror-image as if it were a conspecific (Gallup, 1968), despite the fact that the reflection merely mimics the observer's behavior. Aggressive displays are common and have been elicited by MIS with fish (Lissman, 1932 vide Gallup, 1975), birds (Ritter and Benson, 1934), sea lions (Schusterman, Gentry and Schmook, 1966), primates (Schmidt, 1878 vide Gallup, 1975) and marmots (Svendsen and Armitage, 1973). Additional evidence that the image is interpreted as a conspecific comes from findings such as the fact that isolated ring doves will not lay eggs unless given either the cpportunity to see other doves or to view their own reflection (Lott and Brody, 1966). Mirrors may also promote social facilitation, e.g., behavioral enhancement due to the mere presence of others. Chickens, for example, eat significantly greater amounts of food in the presence of other chickens than in isolation. Substituting a mirror for a companion produces the same enhancement effect (Tolman, 1965). Such evidence suggests that a mirror-image may have the same psychological significance as another

member of the species (Gallup,1975).

MIS not only simulates a conspecific, but, for an individualinexperienced with MIS, apparently simulates an unfamiliar conspecific (Gallup,1975). An animal confronting its own image for the first time would be expected to show responses similar to those given in the presence of a stranger. This expectation is supported by a number of observations. Adult male pigtailed macaques, for example, have a distinctive social display in the presence of an unfamiliar male which consists of crouching, retracting the scalp, and protruding the lips. This display occurs rarely in a well-established colony, but can be induced by a mirror-image (Gallup,1975). Similarly, the dominant chicken from a well-established flock will attack its reflection even though aggression within the flock was minimal (Gallup, 1975).

The similarity of MIS to a natural social encounter is limited by the following constraints:

1. MIS can only approximate the reactions of the test individuals towards animals of identical appearance, presumably those of the same sex, age, and size. Such limited interactions would normally play but a minor role in an individual's total social repertoire.
2. The behavior of the mirror-image is self-induced; the perfect correlation between the behavior of the test animal and that of its mirror-image would never be found in a natural social encounter.

3. The physical properties of mirrors result in apparent distortions in the speed of movements perpendicular to the mirror surface (Gallup, 1968).
4. MIS testing is most conveniently performed within some sort of enclosure: the animal's reactions to the mirror-image may, therefore, be confused with its reactions to the test environment alone.

Some of these limitations could be overcome by the use of forced paired encounters (Krebs, 1970). MIS, however, holds a number of advantages over forced paired encounters: it minimizes the confounding stimuli such as odor and the potential for physical damage, and eliminates the variability of response due to the presence of a second animal. Multiple behavioral measures would undoubtedly provide the most precise behavioral characterizations, but are impractical for field studies where minimal disruption of the animal's normal social activity is desirable. The entire MIS testing procedure, including transporting animals to and from the apparatus, took less than one hour per squirrel and did not appear to interfere with subsequent social activity. Svendsen and Armitage (1973) claimed never to have observed a change in social behavior due to trapping, marking or MIS procedures in 11 years of fieldwork. MIS therefore appeared to provide an excellent opportunity to observe ground squirrels under controlled experimental conditions without unduely influencing their behavior in the field. It also provided an opportunity for

comparison with the work of Svendsen and Armitage (1973).

III. METHODS

The study area bordered the eastern boundary of Waterton Lakes National Park in southwestern Alberta (elevation=1300m). The site consisted of heavily grazed ranchland dominated by fescues (Festuca scabrella and Festuca idahoenis), with patches of shrubs (Amelanchier alnifolia, Potentilla fruticosa, and Rosa woodsii) and trees (Populus tremuloides and Populus balsamifera). Columbian ground squirrels occurred here in a variety of densities and grouping patterns and in both open and shrubby habitats.

All animals used for MIS testing were classified according to their habitat or grouping pattern as "colony", "satellite", or "shrub" residents. For want of a better term, these three classifications are hereafter referred to as "socioecological situations". Animals living alone or in pairs were categorized as "satellite" residents (Svendsen and Armitage, 1973) if their burrow system was a minimum of 500 meters from the nearest occupied burrow system. "Colony" residents were those living in a group consisting of a minimum of three other adults occupying burrows no more than 50 meters apart. Both colony and satellite residents lived in open, heavily grazed habitat with minimal shrub cover. "Shrub" residents lived within dense thickets and thus were essentially unobservable. (This category could include both satellite and colonial grouping patterns.) Trapping data suggested that densities within shrubby habitat were even higher than those within colonial situations (Table 1). .

Table 1. Densities of adult ground squirrels in open colonial and dense shrub situations.[1]

Dense Shrub Situations	Year	Density* (Squirrels/Ha)
Location 1	1977	18
Location 3	1976	22
Location 4	1977	21
Location 6	1976	26
Open Colonial Situations	**Year**	**Density (Squirrels/Ha)**
Location 2	1977	12
Location 3	1977	13
Location 5	1976	12
Location 7	1976	14

[1] ... All locations were between 1 and 2.5 hectares.

* ... Densities include only animals which were recaptured at least once at the same site.

All animals exposed to MIS were marked individuals which had been previously trapped at the same site and were presumed residents.

Trapping and Marking

Squirrels were captured in National live traps (15 x 15 x 50 cm) and earmarked with numbered metal ear tags (National Band and Tag Company: Monel #1). Individuals that were regularly observed were also marked by attaching colored plastic disks to the eartags and by painting unique patterns on the body with hairdye (Lady Clairol Nice N'Easy Blue-Black). Sex, weight, reproductive status, and general condition were recorded before animals were released at the site of capture.

MIS Apparatus and Testing Procedure

The MIS apparatus consisted of a meter square arena with a mirror (90 cm x 90 cm) attached to one wall and covered by a removable partition. Observations were made from a platform built in a tree three meters above the arena. The top of the arena was covered with hardware cloth to prevent escapes, yet permit viewing. The apparatus was located in an aspen grove uninhabited by ground squirrels; thus the effects of other squirrels' scents and vocalizations on the test animals were minimal. The arena was also washed down with Lysol between tests to minimize scent cues from the previous test animal. Each animal was

trapped immediately prior to testing and and released immediately thereafter where trapped.

Both the MIS apparatus and the methodolcgy of mirror exposure and scoring were similar to those used by Svendsen and Armitage (1973) for marmots. Aspects unique to this study included the absence of food in the arena (eating was rarely observed in preliminary tests), the recording of behavior patterns prior to mirror exposure, and the number and types of behavioral categories.

Each animal was allowed a five minute initial adjustment period in the arena, after which its activites were recorded for 10 minutes with the mirror covered. Twenty-three behavioral categories (Table 2) were scored using one-zero sampling (Altman, 1974). The occurrence or non-occurrence of each behavior was scored each minute; scores per minute were added to give a maximum of 10 for each behavior.

MIS was initiated after the animal had been allowed to adjust to the arena with the mirror covered for a full 15 minutes. The partition was removed only when the animal was facing the mirror. The test animal's activities were then recorded for 15 minutes to give a maximum score of 15 for each behavior. Thirty-one behavioral categories were scored during MIS - including the 23 used for the premirror period plus eight specific to the MIS situation (Table 2). These 31 categories represented all but the rarest of those recorded in preliminary observations and included 19 behaviors which

Table 2. Behavioral Categories Recorded During MIS.

Code	Description of Behavior
+CH	Chirping, soft chirp (Betts, 1976).
AC	Alarm calling (Sherman, 1977); shrill chirp (Betts, 1976).
+TC	Tooth chatter, tooth clatter (Betts, 1976).
+ST	Sitting, slouched sit, upright slouch (Betts, 1976).
SD	Standing, quadrupedal position, body horizontal.
AP	Alert position, up alert (Balph and Stokes, 1963), standing upright on hind legs.
+LC	Lying or crouching, entire body apparently touching ground.
+EX	Exploring, arena investigation.
TFL	Tail Flaring, "bushed" tail (Betts, 1976).
+TFK	Tail Flicking, tail wagging.
+M	Motionless, freezing at sight of mirror.
+G	Grooming, maintenance activities.
SS	Sniffing or scratching at walls or floor of arena.
J	Jumping, escape attempts.
BW	Bipedal walking.
*TM	Touching mirror, body contact with mirror other than nosing or pawing and muzzling.
+F1/3	Activities occurring in front third of arena near mirror.
M1/3	Activities occurring in middle third of arena
+R1/3	Activities occurring in rear third of arena away from mirror.
CR	Activities occurring in rear corners of arena.
EA	Activities occurring over entire arena, rapid changes of location.
+*T	Time to approach; score represents the minute during exposure when the animal approached to within 5 cm of mirror.
+*N	Nose contact with image.
+*PM	Pawing and muzzling at image.
*PW	Walking (pacing) parallel to image.
+*AW	Approach/Withdraw - short steps forward followed by steps backwards.
+*LG	Lunging at image.
+OT	Orientation towards image.
+OP	Orientation parallel to image.
+OA	Orientation away or none.
+*RR	Rapid retreat from image, animal either jumps backwards or turns and runs into back wall.

* ... Categories unique to MIS situation.
\+ ... Categories equivalent to or very similar to those used by Svendsen and Armitage (1973).

appear equivalent to those recorded by Svendsen and Armitage (1973) (Table 2).

Experimental Animals

A total of 188 ground squirrels were tested at least once with MIS during the summer of 1977. To assess the repeatability and consistency of MIS, a number of animals (Table 3) were retested from one to four times during the summer. Retests were restricted to colonial and satellite animals that were regularly observed in the field. Seventy-five tests were performed on 20 adult females; detailed field observations were also recorded for 15 of these females, henceforth referred to as the "core group". Thirteen males from both adult and yearling age classes were also retested. All tests were performed between 08:00 and 16:00-18:00 hours during the following time periods:

1. May 1 - May 5: Preparturition
2. June 1 - June 5: Lactation
3. June 14 - June 17: Post-Juvenile Emergence
4. July 1- July 4: Prehibernation.

To better assess the variability of MIS responses, another 155 animals were exposed to MIS between July 15 and July 25. These animals included individuals from different sex and age classes as well as from the three socioecological situations (Table 4).

Table 3. Sex, age and socioecological situation of animals used in repeat MIS tests.

Socioecological Situation	Sex and Age Classes: Adult Female	Adult Males	Yearling Males	Total
Colony	10	3	1	14
Satellite	10	7	2	19
Total	20	10	3	33

Table 4. Sex, age and socioecological situation of animals used in single MIS tests.

Socioecological Situation	Sex and Age Classes				
	Juv. Male	Adult Male	Juv. Female	Adult Female	Total
Shrub	9	10	11	16	46
Colony	10	15	18	22	63
Satellite	10	6	14	14	44
Total	29	31	43	52	155

Yearlings were grouped with adults because separation of the two age classes was unreliable this late in the season. These tests were conducted throughout the daylight hours.

Field Observations

Extensive social behavior and activity pattern data were collected for the "core group" of adult females. These 15 animals were chosen because they were readily observable due to the physical characteristics of their home ranges and because they had occupied approximately the same home ranges the previous year. Data were collected using Focal Animal sampling (Altman, 1974), with a single animal observed per sample period. The frequency and the duration of 14 behaviors (Table 5) were recorded during each sample period. Additional information recorded during social interactions included (a) the identity of the other animal when possible, (b) which animal initiated the interaction, and (c) the type of interaction. The location of the focal animal was recorded at five minute intervals.

The basic sampling regime involved seven 60-minute sampling periods per day for seven days. With a different animal observed during each sample period, this schedule provided a minimum of three observation hours per animal per week over approximately eight weeks between April 20 and June 30. With the addition of supplementary observations made by an assistant, total observation times per animal ranged from 24 to 30 hours. Each squirrel was observed for

Table 5. Behavioral variables recorded during or calculated after focal animal sampling.

Behavior Code	Description
G	Grooming, maintenance, body-scratching, dust-bathing.
R	Resting, crouching, lying down, sunning; body may be partly in burrow.
N	Nest gathering, collecting grass, stuffing nest material into mouth, running to burrow with mouth full of nesting material.
L	Locomotion, trotting or running with head up, nothing in mouth (Dunford, 1977).
AC	Alarm calling (Sherman, 1977), shrill chirp (Betts, 1976).
CH	Chirping, soft chirp (Betts, 1976).
A	Alert position, up alert (Balph & Stokes, 1963); standing upright on hind legs; includes upright slouch and vertical positions (Betts, 1976).
E	Exploring, investigating: rapid movement from burrow to burrow, sniffing burrow entrance, descending partway into burrow (Betts, 1976). Steiner, 1970b).
S	Sitting, slouched sit, sitting on rump with rear feet sticking out in front and stomach protruding.
D	Digging (Betts, 1976; Steiner, 1970b).
P	Proximity; focal animal observed less than two squirrels lengths from another squirrel without a subsequent interaction.
Ft	Total feeding: feeding in all positions with or without locomotion.
Fe	Erect feeding: standing on hind legs while feeding.

Table 5. Continued

Behavior Code	Description
ST	Total social interactions with adults or yearlings; rate per hour.
Sam	Amicable interactions with adults; greeting, allogrooming, mounting, playing, genital sniff; number of amicable interactions divided by total number of interactions.
Sag	Agonistic interactions with adults; broadside displays, chases, fights; number of agonistic interactions divided by total number of interactions.
Sav	Avoidance interactions with adults; moving out of path of approaching squirrel, diving into burrow at approach, crouching while another squirrel passes; number of avoidance interactions divided by total number of interactions.
Sin	Number of interactions initiated by focal animal divided by total number of interactions.
CHR	Number of chases in which focal animal was the chaser divided by total number of chases.
SJ	Total social interactions between focal animal and juveniles; rate per hour.
SJag	Agonistic interactions between focal animal and juveniles; number of agonistic interactions with juveniles divided by total number of interactions with juveniles.

one morning, one mid-day, and one late afternoon sample period per week.

IV. MULVARIATE ANALYSIS OF MIS DATA

The advantages of multivariate statistical techniques for analyzing animal behavior data are now well documented (Aspey and Blankenship, 1977; Maurus and Pruscha, 1973; Morgan et al., 1974). Basically, multivariate techniques can be used for:

1. revealing groups within which individuals are more similar than between groups and
2. identifying relationships among variables.

Such data reduction is particularly valuable when the underlying biological basis of individual variation is unknown (Aspey and Blankenship, 1977), as is true of MIS-induced behavior.

Behavioral data are unlikely to satisfy the strict assumptions of many multivariate techniques in even the best of circumstances. Unfortunately, few authorities answer the question of how far a data set can deviate from the assumptions before the results of a particular test become suspect. It is also no easy matter to know when a data set does satisfy assumptions; for instance, even if each single variable has a normal distribution, the data set as a whole may not have a "multivariate normal distribution" (Puri and Sen, 1971). Not all of the 31 variables used in MIS had normal distributions, but no single transformation was feasible for all variables. Rather than subject the data to a series of different transformations, I decided to use the raw data and trust the robustness of the statistical

procedures.

The MIS data did not meet all the assumptions of the multivariate techniques used. However, as Harris (1975) points out, these strict assumtions are "almost certainly not valid for any real set of data - and yet are nearly valid for many sets of data." Moreover, the fact that a particular assumption was used to derive a test does not mean that a violation of that assumption invalidates the test (Harris,1975; Ito,1969). Most multivariate statistical techniques appear to be very robust to departures from assumptions (Harris, 1975, Chapter 8). The multivariate generalization of the central limit theorum shows that vectors of sample means have a multivariate normal distribution for sufficiently large sample sizes (Ito,1969). Similarly, the assumption of equal covariance matrices (which holds for Hotelling's T^2 and discriminant analysis) may be violated with little effect on significance levels if group sample sizes are large and equal (Ito and Schull,1964). Just how large is "sufficiently large" is much disputed, but seldom answered. Pimentel and Frey (1977) suggest that 25 individuals per group should be adequate. Statisticians with the Educational Research Institute at the University of Alberta recommended a minimum size of 50. The sample sizes used in this analysis were much larger than either of these suggested minima and only equal size groups were compared: the multivariate analyses should therefore yield valid results.

The classification section of the analysis used two techniques, linear typal analysis and cluster analysis, based on very different sets of assumptions. Linear typal analysis is subject to the usual assumptions of the multivariate linear model, whereas cluster analysis methods are based on fewer and less rigid assumptions (Morgan et al., 1975), the specific nature of which depend upon the algorithm. I hoped that the two different classification techniques would reinforce one another (as suggested by Aspey and Blankenship, 1977) while also providing different perspectives for data interpretation.

The multivariate analysis of MIS data may be broken down into the following basic steps:

1. R-factor analysis was used to determine whether or not the behaviors observed before and after mirror exposure could be associated in some meaningful pattern.
2. Linear typal analysis and cluster analysis were used as classification techniques to determine structure among individuals.
3. Discriminant analysis was used to verify the distinctness of the groups identified by linear typal analysis and cluster analysis.

R-Factor Analysis

Factor analysis is a multivariate technique most frequently used to identify relationships among variables. It does so by reducing an original set of correlated variables tc a smaller set of uncorrelated factors. The

factors, each representing a different source of variation, account for a large proportion of the original variance and may be regarded as "primary dimensions of individual differences" (Aspey and Blankenship, 1977).

Factor analysis, however, provides only a general strategy for distinguishing patterns of variation; the particular pattern depends upon the arrangement of the data matrix. While R-factor analysis effectively summarizes the interrelationships among variables, Q-factor analysis groups similar individuals; its focus is essentially typological. The typological use of Q-factor analysis has been heavily criticized on theoretical grounds (Overall and Klett, 1972). On a purely practical level, Q-factor analysis is often misused because a stable factor solution requires a data matrix with a large number of rows relative to the number of columns (Gorsuch, 1974). That there is some confusion concerning the two techniques is apparent from Svendsen and Armitage's 1973 paper wherein they describe a matrix arranged for R-factor analysis, but then present results more appropriate to a Q-factor analysis.

Four data matrices were subjected to R-factor analysis to determine whether behaviors could be reduced to a smaller set of comprehensible factors:

1. The matrix representing the 10 minute observations with the mirror covered: 23 behaviors x 271 cases.
2. The matrix representing the first 10 minutes of observations with the mirror exposed: 23 behaviors x 271

cases.

3. The matrix representing the last ten minutes of observations with the mirror exposed: 23 behaviors x 271 cases.
4. The matrix representing the full 15 minutes of observations with the mirror exposed: 31 behaviors x 271 cases.

The first three matrices were used to provide comparative data on behaviors observed before and after mirror exposure. The eight behavioral categories specific to MIS were eliminated for the comparison. The first and last ten minutes of MIS produced very similar factor solutions. To simplify the presentation, therefore, only the results from the last ten minutes will be presented. The last 10 minutes of MIS observations should provide the most conservative comparison since initial reactions to mirror exposure may have been responses both to the mirror-image itself and to the movement of the partition and/or the sudden flash of the reflective surface.

A matrix of product-moment correlation coefficients was computed for each data matrix. Eigenvalues, indices of how much variance is accounted for by each factor, were extracted from the correlation matrix and only those greater than 1.0 were used to determine the factors (as recommended by Guttman,1954 vide Gorsuch,1974). Factors were extracted until the communality estimates (communality = the proportion of a variable's total variance that is accounted

for by a factor) stabilized and the factor matrix was then rotated to simple structure using Kaiser's normal Varimax method (Kaiser, 1958 vide Gorsuch, 1974). All factor analyses were performed using the SPSS (pa2) computer program.

Factor loadings represent the degree and direction of the relationship of the variables to the factors. Following the guidelines suggested by Comrey (1973), 0.350 was considered the zero factor loading (i.e., the lower cutoff value for indicating factor loadings) and only loadings 0.450 and higher were considered in factor interpretations.

Results of R-Factor Analysis for the 10 Minute Period Before Mirror Exposure

Seven factors, accounting for 71.3% of the total variance, were extracted from the data matrix representing the period with the mirror covered (Table 6). Factor I was interpreted as "Active/Inactive" since it had high positive loadings on general activity measures and high negative loadings on behaviors such as Motionless. Factor II was an orientation factor which loaded positively on Orientation Away From Mirror Or None and negatively on Orientation Parallel to Mirror. Since the mirror was not influencing orientation, this factor may be regarded as a simple contrast between frequently changing and constant orientations. Factor III, "Tail Movement", had high positive loadings on both Tail Flicking and Tail Flaring. Factor IV, "Corner Location", had a very high positive loading on the

Table 6. Varimax rotated factor matrix based on 23 behaviors exhibited during the 10 minute period with the mirror covered.*

	Factors						
Behaviors	F1	F2	F3	F4	F5	F6	F7
Chirp	-0.450						
Alarm Call			0.393				
Tooth Chatter							
Sitting						0.469	
Standing							
Alert Position	0.819						
Lying/Crouch	-0.561						
Exploring	0.898						
Tail Flare			0.758				
Tail Flick			0.711				
Motionless	-0.876						
Groom	0.575						
Sniff/Scratch	0.854						
Jump	0.586						
Bipedal Walk	0.733						
Front 1/3	-0.608						
Middle 1/3						0.544	
Rear 1/3							
Rear Corner				0.981			
Entire Arena	0.768						
Orient Towards					-0.789		
Orient Parallel		-0.903					
Orient Away		0.849			0.426		
% Total Variance	31.9	10.2	7.8	6.3	5.5	5.1	4.6
% Cum. Variance	31.9	42.1	49.9	56.2	61.6	66.7	71.3

* Zero factor loading is 0.350 throughout.

variable of the same name. Factor V was another orientation factor which was difficult to interpret given the absence of the mirror-image, but which appeared to reflect an affinity for the rear portion of the arena. Factor VI was associated with Tooth Chattering and middle arena locations. Factor VII had no loadings high enough for reliable interpretation.

Results of R-Factor Analysis for the 10 Minute Period After Mirror Exposure

Six factors, accounting for 66.3% of the total variance, were extracted from the data matrix representing the last 10 minutes with the mirror exposed (Table 7). Factor I showed a similar loading pattern to the previous Factor I and was also interpreted as "Active/Inactive". Factor II, designated "Alarm/Excitement". had positive loadings on Alarm Calling, Tooth Chattering, Tail Flicking and Tail Flaring. Factor III, "Corner Motionless/Front Active", contrasted animals which crouched quietly in the corners furthest from the mirror and those which engaged in various activities in the front of the arena near the mirror. Factor IV was readily interpretable as "Orientation Towards the Mirror". Factor V, "Rear of the Arena", represented locations in the rear third of the arena other than the corners. Factor VI was the least interpretable, with a high negative loading on Middle Third of Arena.

Table 7. Varimax rotated factor matrix based on 23 behaviors exhibited during the 10 minute period with the mirror exposed.*

Behaviors	Factors F1	F2	F3	F4	F5	F6
Chirp						
Alarm Call		0.516				
Tooth Chatter		0.661				
Sitting			0.529			
Standing						-0.416
Alert Position	0.561					
Lying/Crouch	-0.396		-0.732			
Exploring	0.836					
Tail Flare		0.548				
Tail Flick		0.970				
Motionless	-0.560		-0.609			
Groom	0.459		0.447			
Sniff/Scratch	0.654		0.379			
Jump						
Bipedal Walk	0.513					
Front 1/3			0.785			
Middle 1/3						-0.758
Rear 1/3					0.897	
Rear Corner			-0.715			0.355
Entire Arena	0.807					
Orient Towards				0.927		
Orient Parallel			0.573			
Orient Away				-0.478		
% Total variance	27.9	14.0	7.9	6.0	5.5	5.1
% Cum. Variance	27.9	41.8	49.8	55.8	61.3	66.3

* Zero facor loading is 0.350 throughout.

Comparison of 10 Minute Periods Before and After Mirror Exposure

Though comparison of the two sets of factors representing behavior before and after mirror exposure reveals obvious qualitative similarities and differences, the relationships between the two sets of factors can also be quantified. According to Gorsuch (1974), two factors are related to the degree that they correlate when scored for an appropriate set of individuals. Since the same individuals and variables were used for both factor analyses, product-mcment correlation coefficients can be computed between any two sets of factor scores representing factors with similar loading patterns (Table 8). Perfect correlation between factors could occur only if both the factors and the individuals were unchanged over the given time period (Pinneau and Newhouse, 1964 *vide* Gorsuch, 1974).

Three significant correlations were found between factors. The correlations between the first factors suggests that the activity levels of individuals were similar before and after mirror exposure. The highest correlation was between Factor III from the period with the mirror covered and Factor II from the period with the mirror exposed: both factors involved Tail Flicking. Less comprehensible is the correlation between the sixth factors from the two periods: Tooth Chattering prior to mirror exposure was related to an intermediate arena location during MIS.

Hotelling's T^2, the multivariate analogue of the

Table 8. Correlations[1] between factors[2] representing behaviors before and after mirror exposure.

Before Mirror Factors	After Mirror Factors					
	F1	F2	F3	F4	F5	F6
F1	0.273*					
F2						
F3		0.576*				
F4			-0.001			
F5				-0.083		
F6						-0.189*
F7			-0.068		0.055	

1 Pearson's r calculated from factor scores for the same set of animals.

2 Correlations are shown only between factors with some similarity of loading pattern.

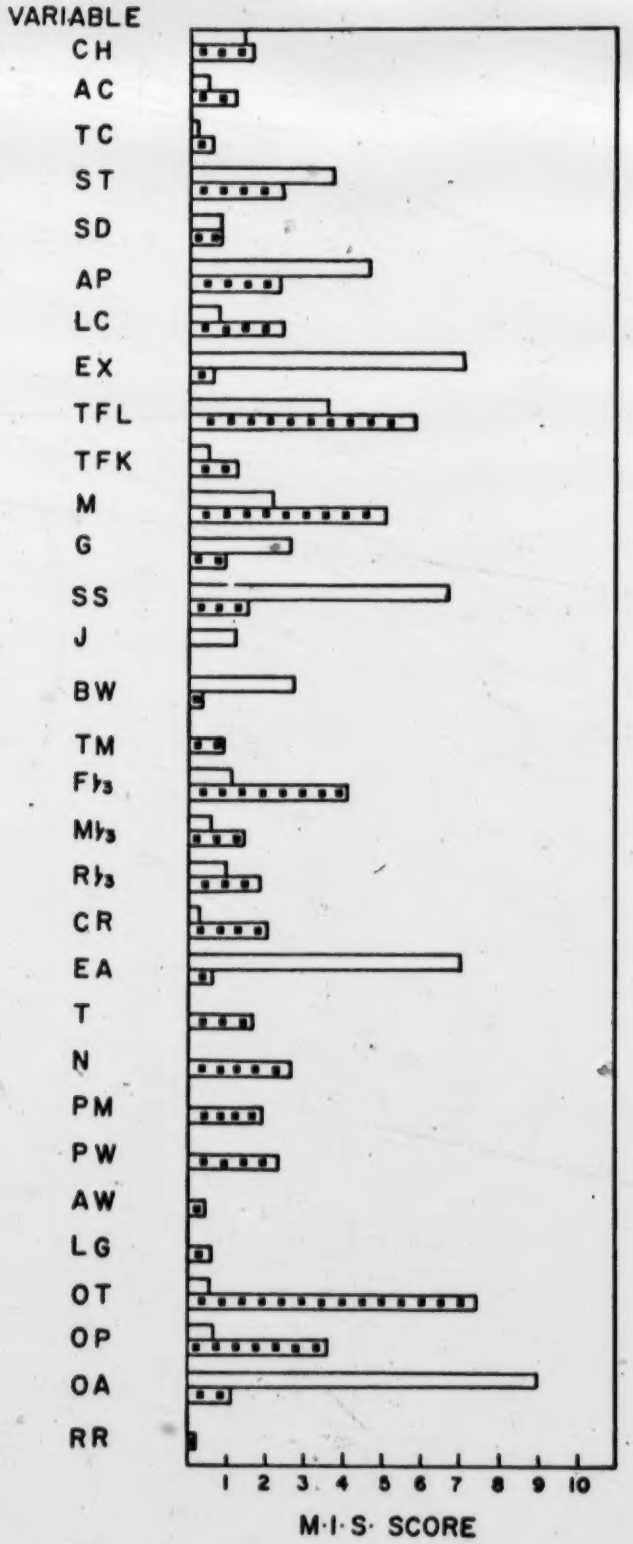
* Significant at p=0.05 or less.

student's t test, allowed a direct test of the null hypothesis cf no change between periods before and after mirror exposure. XDERS program MULV06 is a dependent sample Hotelling's T^2 which can be used to compare a sample of means against the population set of means. Scores from the 10 minutes prior to mirror exposure were subtracted from the scores from the last ten minutes of MIS and the differences were used as input for MULV06. The vector of these sample means was then tested against the null vector of population means.

The T^2 analysis resulted in rejection of the null hypothesis cf no difference between periods (T^2 = 201.938, p = 0.000). This difference between periods might be expected simply because an additional set of behaviors was possible with the mirror exposed. Figure 1 shows the mean profiles for the 10 minute periods before and after mirror exposure - including those additional behaviors specific to MIS.

Examination of individual behavioral variables shows that mirror exposure produced changes not easily explained by the addition of a new set of behaviors. Behaviors such as Alert Position, Exploring, Grooming, and Sniffing and Scratching decreased dramatically after mirror exposure, while Lying and Crouching, Tail Flicking, Tail Flaring, and Motionless increased. Concommitant with the decrease in Exploring was a decrease in movements over the entire arena; animals were more likely to remain in a single location after mirror exposure. Orientation patterns changed such

Figure 1. Mean profiles from 10 Minute periods before and after mirror exposure. Empty bars represent the period before mirror exposure. Bars with squares represent the period after mirror exposure.


VARIABLE
CH
AC
TC
ST
SD
AP
LC
EX
TFL
TFK
M
G
SS
J
BW
TM
F⅓
M⅓
R⅓
CR
EA
T
N
PM
PW
AW
LG
OT
OP
OA
RR
1 2 3 4 5 6 7 8 9 10
M·I·S· SCORE

that orientations directed towards or parallel to the mirror increased, while non-mirror directed orientations decreased sharply.

Comparison of the two factor solutions reveals other more subtle changes in overall behavior patterns. Alarm/excitement related behaviors, for example, accounted for a much higher proportion of the variance after mirror exposure than they did before. The factor solution for the period after mirror exposure also revealed a previously unseen division between animals that crouched quietly in rear corners and those that were active in the front of the arena (in the vicinity of the mirror).

Results of R-Factor Analysis for the Full 15 Minutes of MIS

The third R-factor analysis, representing the full 15 minutes of MIS, reduced the 31 behavioral categories to eight factors accounting for 69.9% of the total variance (Table 9). Factor I represented the contrast between active, mirror contact behaviors and inactive, mirror-avoidance behaviors and was labeled "Contact/Avoidance". Factor II, with high positive loadings on Tooth Chattering and Tail Flicking was interpreted as "Excitability/Aggression". Factor III was designated "Arena Investigation". Factor IV, interpreted as "Conflict", was associated with Approach/Withdrawal and very rapid retreats from the mirror. Factor V represented locations in the rear third of the arena - other than corners. Factor VI was not readily

Table 9. Varimax rotated factor matrix based on 31 behaviors exhibited during MIS.*

Behaviors	Factors F1	F2	F3	F4
Chirp				
Alarm Call		0.452		
Tooth Chatter		0.746		
Sitting				
Standing				
Alert Position	0.619			
Lying/Crouch	-0.623			
Exploring	0.516		0.680	
Tail Flick		0.455		
Tail Flare		0.929		
Motionless	-0.799			
Groom	0.555			
Sniff/Scratch	0.759			
Jump				
Bipedal Walk	0.482			
Touch Mirror	0.509			
Front 1/3	0.778			
Middle 1/3				
Rear 1/3				
Rear Corners	-0.467			
Entire Arena	0.392			0.423
Time to Approach				
Nose	0.946			
Paw/Muzzle	0.903			
Parallel Walk	0.939			0.722
Approach/Withdraw		0.453		
Lunge				
Orient Towards				
Orient Parallel			0.452	
Orient Away				0.792
Rapid Retreat				
Total Variance	29.2	11.7	6.7	6.1
Cum. Variance	29.2	40.9	47.6	53.7

* Zero factor loading is 0.350 throughout.

Table 9. Continued

	Factors			
Behaviors	F5	F6	F7	F8
Chirp				
Alarm Call				
Tooth Chatter				
Sitting			0.747	
Standing		-0.455		
Alert Position				
Lying/Crouch		0.547		
Exploring				
Tail Flick				
Tail Flare				
Motionless				
Groom				
Sniff/Scratch				
Jump				
Bipedal Walk				
Touch Mirror			0.419	
Front 1/3			0.388	
Middle 1/3		-0.494		
Rear 1/3	0.789			
Rear Corners		0.559	-0.434	
Entire Arena				
Time to Approach		-0.366		
Nose				
Paw/Muzzle				
Parallel Walk				
Approach/Withdraw				
Lunge				
Orient Towards				0.891
Orient Parallel				
Orient Away		0.354		
Rapid Retreat				
Total Variance	4.8	4.2	3.9	3.2
Cum. Variance	58.5	62.7	66.7	69.9

*Zero factor loading is 0.350 throughout.

interpretable due to the low loadings, but was related to lying quietly in the rear corner of the arena. Factor VII was simply interpreted as "Sitting". Factor VIII represented "Orientation Towards the Mirror".

Description of Columbian Ground Squirrel Responses to MIS

Columbian ground squirrel responses to MIS were very similar to the marmot responses described by Svendsen and Armitage (1973) in spite of dissimilar analyses. Ground squirrel responses were similarly separable into two extreme patterns of active attempts at social contact with the mirror-image and passive avoidance of such contact. Initial responses to the mirror exposure and/or the movement of the partition were immediate and dramatic: freezing while facing the mirror, frenzied escape attempts, and standing on hind legs while giving alarm calls were all common. Soon after these initial responses, most squirrels either approached or retreated fromm the mirror. Others, however, remained motionless in their original positions, groomed, investigated the arena away from the mirror, or approached and withdrew repeatedly. Animals that approached the mirror would often engage in such distinctly social behaviors as greeting and pawing and muzzling with their mirror-image. Animals that retreated from the mirror often crouched motionless in the corners furthest from the mirror for the full 15 minutes. Ground squirrel responses not described for marmots included lying in the far corners oriented away from

the mirror and walking or "pacing" parallel to the mirror, often with the flank touching the mirror.

Most behaviors observed during MIS appeared to be "other-directed"; the test animals acted as if they were viewing ancther animal. A few ground squirrels were even observed apparently trying to look behind the attached mirror for the "other" animal. The responses of ground squirrels to MIS are thus consistent with Gallup's (1975) supposition that MIS represents a social stimulus which simulates the presence of an unfamiliar conspecific. Naturally occurring encounters with unfamiliar conspecifics are rarely observed in the field, yet may play a critical role in determining distribution patterns and social structure. While MIS may not perfectly mimic such encounters, it may provide a general index of social confidence and some indication as to the probable outcome of encounters.

There was no evidence that behavior changes after mirror exposure were a function of habituation to the arena situation. Several behavior patterns frequently recorded during MIS were never recorded in pretest periods. Habituation would presumably act to reduce levels of alarm, whereas alarm-related behaviors such as vocalizations and tail movements actually increased after mirror exposure. Dramatic changes in individual behavior patterns were frequent: individuals that were quiet and inactive during the pretest period would become active and vocal during MIS

and vice versa.

V. CLASSIFICATION OF INDIVIDUALS ON THE BASIS OF MIS RESPONSE

While R-factor analysis reveals the structure within the behavioral variables recorded during MIS, it does not actually indicate which animals behave similarly. The identification of natural groupings among the squirrels based on MIS requires a classificatory or typological approach. There are many statistically legitimate approaches to classification: multidimensional scaling, linear typal analysis, principal components analysis, Q-factor analysis, and cluster analysis are perhaps best known. Each of these basic techniques represents a multiplicity of algorithms - each with limitations and advantages which vary according to the authority consulted. One way out of this statistical morass is to use several techniques and look for congruent results. Different analyses may provide different, but equally valuable perspectives on the relationships between and among groups or classes (Aspey,1976). Cluster analysis and linear typal analysis are the two basic classification techniques used in this study.

Linear Typal Analysis

Linear typal analysis (Overall and Klett,1972) is a classification method mechanically similar to Q-factor analysis, but with minor scaling differences which were designed to correct the usual Q-factor analysis problems. Linear typal analysis assumes that a few hypothetical

"Pure-Types" underlie any heterogeneous group of individuals. Its objectives are to discover the number and nature of these types, to describe the prototype score vectors representing each pure type and to determine the similarities of each observed individual to each pure type.

Linear typal analysis was based on the program presented in Overall and Klett (1972, p 230 - 288) and modified for use with MTS. Program limitations required reduction of the data matrix to 31 variables by 188 cases. The 188 cases represent the initial MIS test of each animal.

Linear typal analysis produced three pure types. Figure 2 depicts the pure type profiles computed as the means of profiles from individuals most closely related to each pure type. The pure types can be considered completely independent only if the "cosine" matrix (intercorrelations between pure types) is an identity matrix. According to Overall and Klett(1972), correlations less than 0.30 are desirable, while those greater than 0.50 should be rejected. The lack of correlations greater than 0.50 in the cosine matrix (Table 10) indicates that the three hypothetical types are quite distinct. Types two and three are the most closely related.

Linear typal analysis also supplies weighting coefficients that specify the relative contributions of the three pure types to each individual. Theoretically, any individual may be a mixture of several types, but the majority will be recognizable as highly similar to a single

Figure 2. Linear typal analysis: pure type profiles.

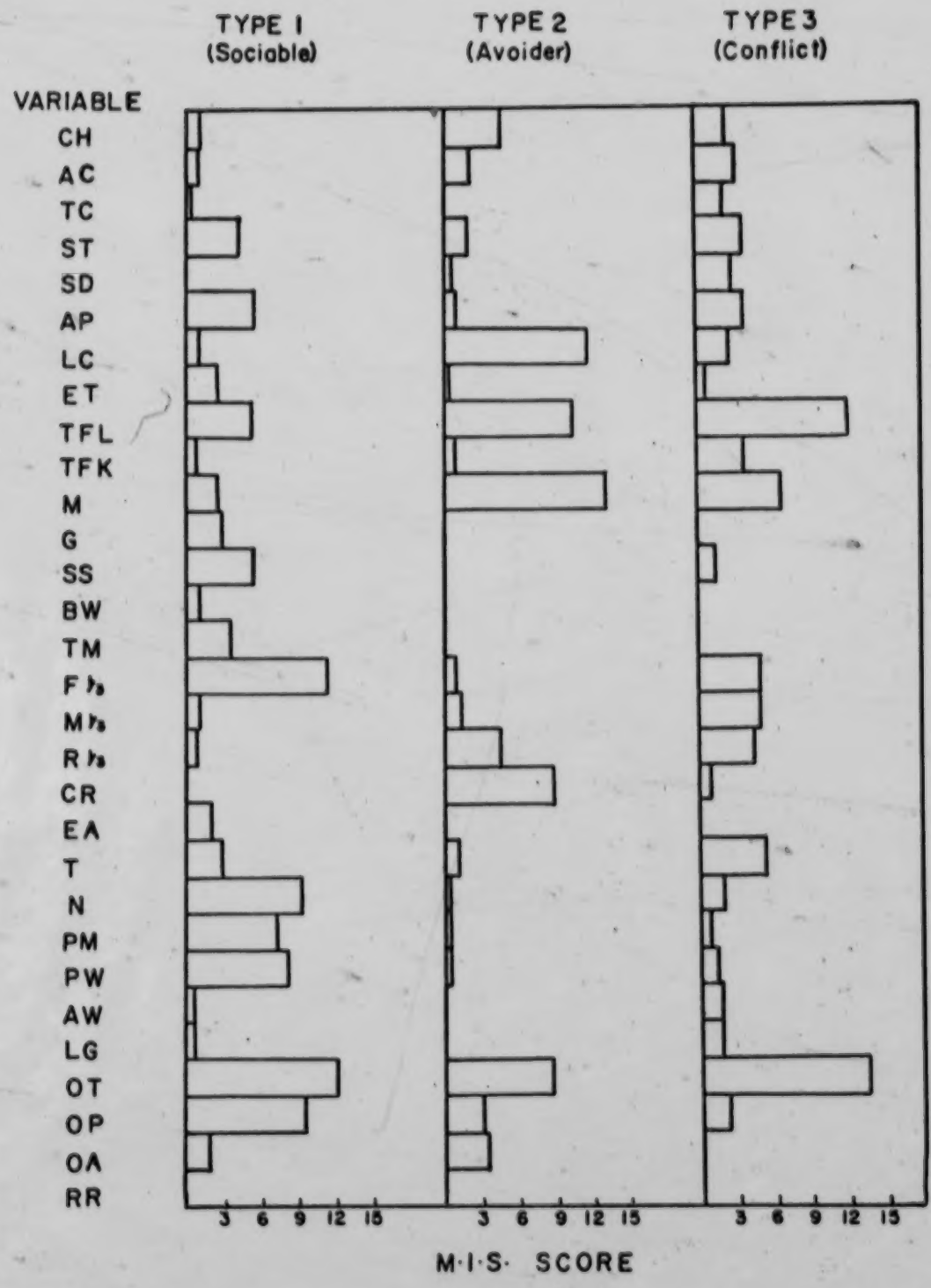

TYPE 1
(Sociable)
TYPE 2
(Avoider)
TYPE 3
(Conflict)
VARIABLE
CH
AC
TC
ST
SD
AP
LC
ET
TFL
TFK
M
G
SS
BW
TM
F ½
M ½
R ½
CR
EA
T
N
PM
PW
AW
LG
OT
OP
OA
RR
3 6 9 12 15
3 6 9 12 15
3 6 9 12 15
M·I·S· SCORE

Table 10. Primary cosine matrix of three pure types extracted from MIS data by linear typal analysis.

	Pure Types		
Pure Types	Type 1	Type 2	Type 3
Type 1	1.000	-0.193	0.025
Type 2		1.000	0.365
Type 3			1.000

pure type. Classification is achieved by assigning each individual to the class represented by the most similar pure type.

Cluster Analysis

The term "cluster analysis" is often used synonymously with "classification" to describe any or all of three general procedures: hierarchical classification, partitioning, and clumping (Cormack,1971). The common objective of all three is the allocation of entities to initially undefined classes so that entities within a given class are somehow more similar than those outside that class. Though that objective may be simple enough, the means of achieving it are legion. There are many potential algorithms for each of the three general procedures and a single algorithm may even combine procedures (e.g. when a hierarchical procedure is subjected to a stopping rule to produce a partition). The novice in the field is presented with a bewildering series of choices between similarity coefficients; hierarchical, centroid, modal, or monothetic divisive techniques; iterative reallocation procedures, and diverse graphical approaches. I chose to use the recommended analyses from the Clustan 1C package (Wishart, 1972) which work on the principle that an optimal solution is best recognized when several different starting groupings produce the same final cluster solutions. Another indicator of a robust cluster solution results when cluster analyses

performed on subsets of a data matrix give similar classes (Anderberg, 1973). Consequently, cluster analyses were performed on two data matrices: the full 31 x 271 matrix and a 31 x 149 matrix created by dropping all retests and all tests from a group of known males. The analysis of the larger matrix uses a series of iterative relocations starting from different random classifications and different similarity coefficients; a satisfactory cluster solution is indicated by equivalent final classifications. The analysis for populations less than 150 involves the following basic steps:

1. Ward's method of hierarchical clustering from a matrix using Euclidean distance as the similarity coefficient,
2. iterative relocation to improve the error sum of squares solution starting from the results of Ward's clustering,
3. comparison of results from Ward's clustering to those obtained via iterative relocation from an initial random classification.

The choice of the optimum cluster number was based on error sum of squares criterion (Davies, 1978; Anderberg, 1973; Wishart, 1971). Error sum of squares (ESS) refers to the total sum of squared deviations within all clusters at a particular aggregation stage - and can be regarded as a measure of the information content of the particular cluster configuration.

If each member of a set of n data units is treated as a separate cluster, then ESS is zero and information content

maximal. If all n units are combined into a single cluster, then the error sum of squares is maximal and information content minimal. Between these extremes the error sum of squares within group is that portion of the total variance not accounted for by the current group of clusters. Each reduction in the number of clusters increases the ESS; a large increase in ESS indicates that the previous cluster configuration was the more "natural." The optimum or most "natural" number of clusters is that which best minimizes distortions of the original data while also reducing the data complexity to the greatest extent (Davies,1978).

Table 11 shows the increase in error sum of squares at selected stages of clustering. The greatest increase in ESS occurred with the fusion to form two clusters: the "optimal" number of clusters was therefore three according to the ESS criterion. Profiles based on the mean cluster scores for each variable were virtually identical to those previously presented for linear typal analysis (Figure 3). (The descriptive statistics for each cluster are presented in Appendix 2.)

Comparison of Classifications Obtained Using Linear Typal Analysis and Cluster Analysis

Linear typal analysis and cluster analysis both grouped individuals into three distinct and equivalent types or classes on the basis of MIS performance. The associations between the three different partitions (based on the

Table 11. Increases of error sum of squares at selected stages of the clustering process.

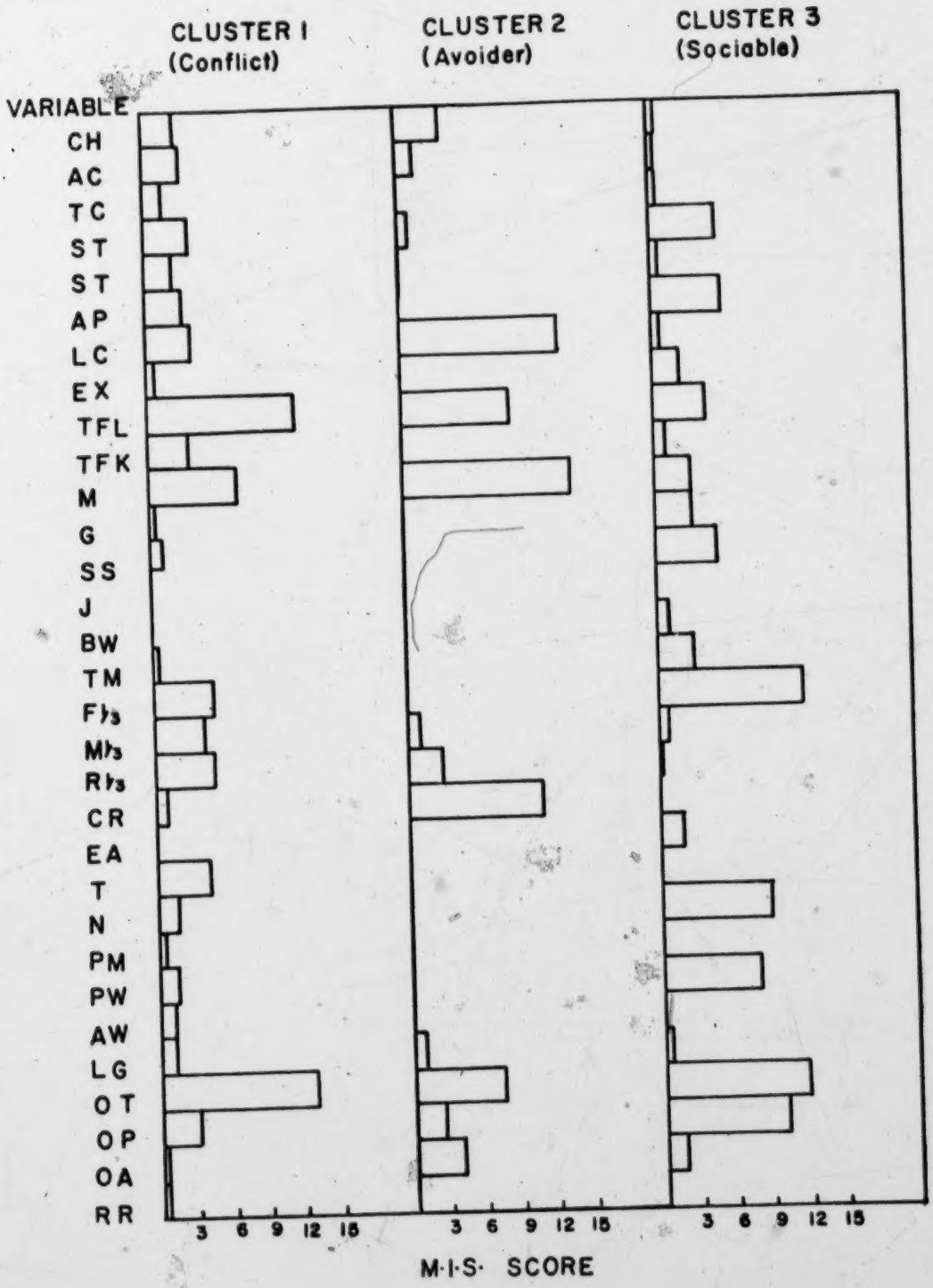
(a) Large Sample Cluster Analysis (N=271)

Number of Clusters	Error Sum of Squares ESS	Increase in ESS Associated with Next Fusion
10	255.2015	10.5658
9	265.7673	12.7456
8	278.5129	12.0258
7	290.5388	14.1028
6	304.6416	17.0520
5	321.6936	22.2190
4	343.9126	25.7866
3	369.6992	49.4917
2	419.1809	

(b) Reduced Sample Cluster Analysis (N=149)

Number of Clusters	Error Sum of Squares ESS	Increase in ESS Associated with Next Fusion
10	133.5223	7.3201
9	140.8424	5.8519
8	146.6759	7.8857
7	154.5616	8.2032
6	162.7648	9.0367
5	171.6847	12.7213
4	184.4060	12.3254
3	196.7314	30.4044
2	227.1354	

Figure 3. Cluster analysis: profiles based on mean cluster scores.


CLUSTER 1
(Conflict)
CLUSTER 2
(Avoider)
CLUSTER 3
(Sociable)
VARIABLE
CH
AC
TC
ST
ST
AP
LC
EX
TFL
TFK
M
G
SS
J
BW
TM
F⅓
M⅓
R⅓
CR
EA
T
N
PM
PW
AW
LG
OT
OP
OA
RR
3 6 9 12 15
3 6 9 12 15
3 6 9 12 15
M·I·S· SCORE

cluster analysis matrix of 149 individuals, cluster analysis matrix of 271 individuals, and linear typal analysis matrix of 188 individuals) were assessed using a simple contingency table approach (Borko, 1968 vide Anderberg, 1973). With this procedure, one can evaluate the predictability of an individual's type membership in the other partition. Contingency tables and associated statistics are presented in Table 12.

Table 13 summarizes the results of the three classification techniques. The distribution of cases among types differs significantly from 1:1:1 only for the classification based on the cluster analysis of the 271 times 31 matrix. However, the partitions based on the cluster analysis of the 149 x 31 matrix and the linear typal analysis of the 188 x 31 matrix may be the more representative of the general population since they eliminate the extra weighting on animals with repeat tests.

Description of MIS-Derived Behavioral Types

Type S or "Sociable" animals were active individuals that interacted frequently with their mirror image. These squirrels spent much of their time in the vicinity of the mirror, but also investigated the arena, groomed, and engaged in other activities when not involved in mirror-contact behaviors. They had consistently low scores on vocalizations and tail movements - suggesting minimal levels of alarm and excitement.

Table 12. Similarities between partitions: contingency tables comparing partitions from cluster and linear typal analyses.

LTA = Linear Typal Analysis,
CA(149) = Reduced Sample Cluster Analysis,
CA(271) = Large Sample Cluster Analysis

(a) Linear Typal Analysis vs Cluster Analysis (271)

	CA(271) Clusters		
LTA Types	Sociable	Avoider	Conflict
Sociable	63	1	7
Avoider	0	44	9
Conflict	2	0	62

Goodnes of Fit Chi.Square=276.64; probability=0.000
Likelihood Ratio Chi.Square=281.87; probability=0.000
* Goodman and Kruskal Lambda=0.8326

(b) Linear Typal Analysis vs Cluster Analysis (149)

	LTA Types		
CA(149) Clusters	Sociable	Avoider	Conflict
Sociable	46	0	0
Avoider	1	40	0
Conflict	5	3	54

Goodness of Fit Chi-Square=249.53; probability=0.000
Likelihood Ratio Chi-Square=258.30; probability=0.000
* Goodman and Kruskal Lambda=0.9011

* Recommended for comparison of partitions (Anderberg, 1973).

Table 13. Comparison of classification results: number of animals in each class.

LTA = Linear Typal Analysis
CA(271) = Large Sample Cluster Analysis
CA(149) = Reduced Sample Cluster Analysis

Classification Method	Cluster or Type: Sociable	Avoider	Conflict
CA(271)	98 (36.2%)	67 (24.7%)	106 (39.1%)
CA(149)	46 (30.9%)	41 (27.5%)	62 (41.6%)
LTA	71 (37.8%)	53 (28.2%)	64 (34.0%)

Type A or "Avoider" animals were inactive, spent considerable time at the back of the arena and did not approach the mirror. Many Type A animals froze at the first sight of their mirror image and remained motionless for the entire 15 minute period. Orientation was usually towards the mirror, but some Type A's faced the corner, thereby avoiding sight of the mirror.

Type C included all individuals who fell in between the two extreme responses of sociability and avoidance. For lack of a better interpretation, they may be described as being in a state of "conflict",i.e. unable to choose between sociable interaction with the mirror-image or avoidance of interaction. Type C included animals with aggressive responses, animals which were hesitant, but eventually contacted the mirror; animals which repeatedly approached and withdrew without ever contacting the mirror; and those which sat or lay near the mirror without interacting with the mirror image. Type C individuals were characterized by high scores on vocalizations and tail movements - suggesting high levels of alarm and excitement.

There are striking similarities between the three MIS types just described and the three "factors" described by Svendsen and Armitage (1973) for marmots. Their "Avoidance" and "Sociability" factors clearly describe the same basic behavior patterns displayed by my "Avoider" and "Sociable" types. Their "Approach" factor appears to include behaviors displayed by Type C individuals and similarly fails to

differentiate between aggressive and socially-positive or neutral individuals. Svendsen and Armitage, however, describe marmots as either Sociable, Avoider, or Aggressive types. These labels do not appear to be consistent with the groups actually differentiated by their statistical analysis. My analysis showed that Type C animals shared many behavioral patterns not obviously related to aggression and I did not, therefore, feel justified in differentiating aggressive individuals from other Type C squirrels. Distinctly aggressive displays were infrequent and of short duration in my study, but were perhaps more frequent in marmots.

Discriminant Analysis

Multiple discriminant analysis is not itself a classification procedure since it assumes that classes have been predetermined. It is, however, often used in conjunction with classification procedures to verify the distinctness of the classes, to determine which variables best discriminate among classes, and to assign new individuals to previously determined classes.

Since the similarity of the two classifications has been established, discriminant analysis results will be presented only for the 31 x 188 data matrix used in linear typal analysis. The type membership as determined by linear typal analysis was entered as a separate variable for each case. Analysis was performed using the SPSS multiple

stepwise discriminant analysis program.

Two discriminant functions were computed which together accounted for 100% of the variance. The first accounted for 76.27% of the variance; the second accounted for 23.78%. The 31 original variables were reduced to the 20 "optimal" variables listed below:

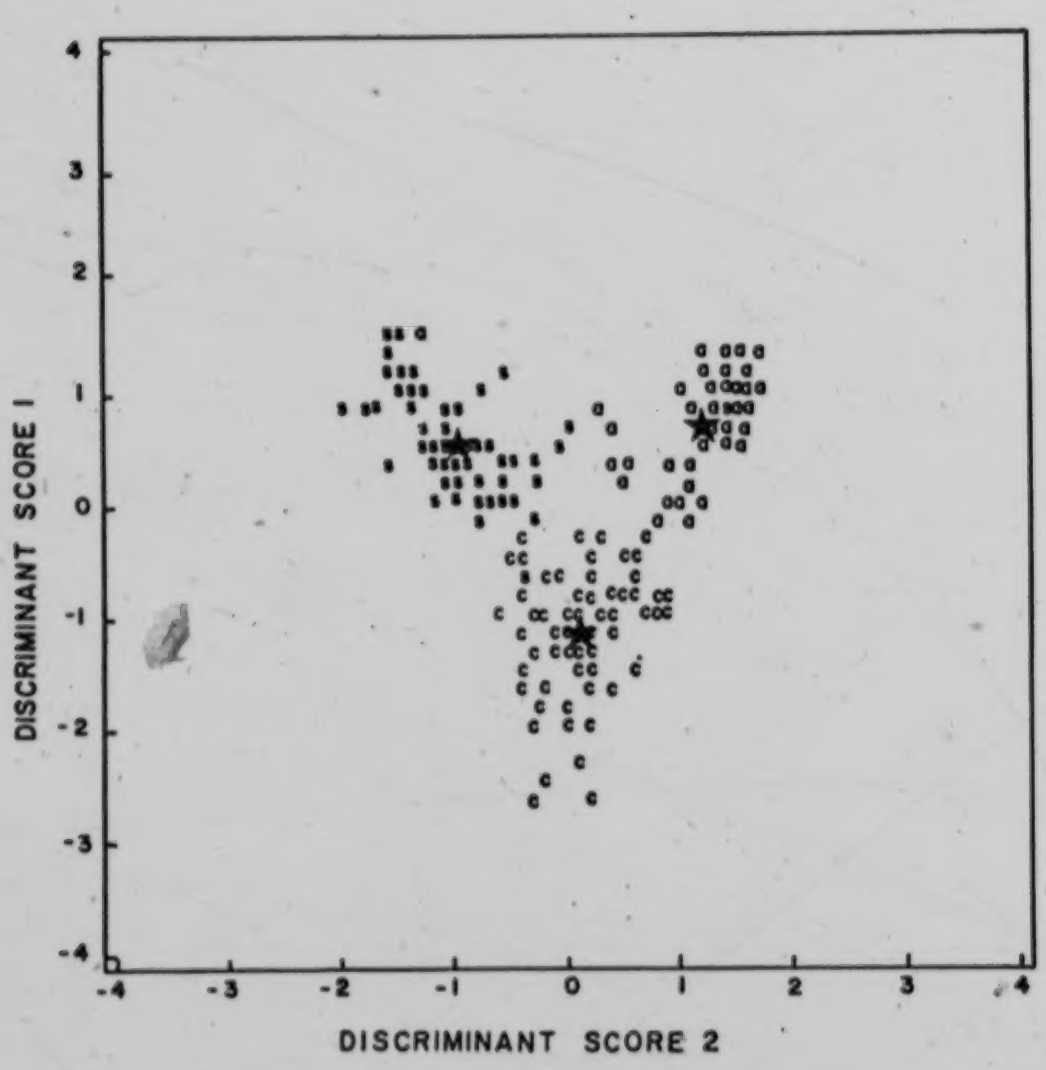
1. Alarm Calling
2. Standing
3. Lying or Crouching
4. Tail Flaring
5. Tail Flicking
6. Sitting
7. Alert Position
8. Exploratory Activity
9. Motionless
10. Grooming
11. Bipedal Walking
12. Touching Mirror with Body
13. Front Third of Arena
14. Middle Third of Arena
15. Time to Approach
16. Nose Contact with Image
17. Pawing and Muzzling Image
18. Approach/Withdraw
19. Orientation Towards the Mirror
20. Orientation Away or None

Predicted type memberships, based on these 20 variables, were 97.87 % correct - indicating that the three types are indeed distinct. Figure 4 shows a scatterplot of the three MIS types against the two discriminant functions: group centroids are represented by stars.

The 83 repeat tests were assigned to the behavioral types derived from linear typal analysis using the SPSS option for classification of new cases. The newly assigned types were identical to those originally obtained via cluster analysis for 82 out of 83 tests.

Discriminant analysis also provided a tool for subsequent analysis: discriminant function scores were used as quantitative indices of type membership to assess the consistency of MIS types over time.

Figure 4. Scatterplot of three MIS types against two discriminant functions. Stars represent group centroids.


DISCRIMINANT SCORE 1
DISCRIMINANT SCORE 2
4
3
2
1
0
-1
-2
-3
-4
-4
-3
-2
-1
0
1
2
3
4

VI. CONSISTENCY OF MIS TYPES OVER TIME

To determine the consistency of MIS-derived types, one needs to know the likelihood of an individual's type changing upon retesting. Thirty-three squirrels were retested at regular intervals over the season. Out of a total of 116 tests, the type at retesting was different in only five cases involving three individuals.

Quantitative evaluation of reliability/repeatability made use of the discriminant function analysis described above. Two discriminant function scores were available for each MIS test; these scores were used to calculate reliability and repeatability indices. SPSS program "Reliability" provided the basic repeated measures analysis of variance. Repeatability was calculated after Becker (1967 *vide* Krebs, 1970). The coefficient of reliability is given as Cronbach's alpha (SPSS update, 1977). Table 14 summarizes the results obtained using the first discriminant function scores; Table 15 is based on the second discriminant function scores.

Both repeatability and reliability indices were high for both sets of discriminant function scores - indicating great consistency of response to MIS. Some squirrels were so consistent that the observer could closely predict the timing and postural components of the approach to the mirror; others varied in the precise sequence and frequencies of behaviors, but were consistent in their general pattern of response. This consistency is

Table 14. Repeated measures analysis of variance based on first discriminant function scores.

(a) Twenty Animals Tested Four Times

Analysis of Variance

Source of Variation	SS	df	Mean Square	F	Probability
Between Animals	75.984	19	3.999		
Within Animals	2.371	60	0.039		
Between Tests	0.027	3	0.009		
Residual	2.394	57	0.041	0.219	0.882
Total	78.355	79	0.992		

Reliability Coefficient, alpha, = 0.9872
Repeatability = 0.9697

(b) Thirty Animals Tested Three Times

Analysis of Variance

Source of Variation	SS	df	Mean Square	F	Probability
Between Animals	91.721	29	3.1628		
Within Animals	5.185	60	0.086		
Between Tests	0.112	2	0.056		
Residual	5.073	58	0.087	0.640	0.531
Total	96.906	89	1.088		

Reliability Coefficient, alpha, = 0.9723
Repeatability = 0.9465

Table 15. Repeated measures analysis of variance based on second discriminant function scores.

(a) Twenty Animals Tested Four Times

Analysis of Variance

Source of Variation	SS	df	Mean Square	F	Probability
Between Animals	76.924	19	4.049		
Within Animals	4.158	60	0.069		
Between Tests	0.056	3	0.019		
Residual	4.102	57	0.072	0.258	0.855
Total	81.082	79	1.026		

Reliability Coefficient, alpha, = 0.9822
Repeatability = 0.9487

(b) Thirty Animals Tested Three Times

Analysis of Variance

Source of Variation	SS	df	Mean Square	F	Probability
Between Animals	72.120	29	2.487		
Within Animals	8.303	60	0.138		
Between Tests	0.015	2	0.074		
Residual	8.288	58	0.143	0.052	0.949
Total	80.423	89	0.904		

Reliability Coefficient, alpha, = 0.9425
Repeatability = 0.8967

particularly noteworthy because behavioral patterns of ground squirrels are seldom constant or independent of seasonal influences (A. Wroot, personal communication). I observed no change in scores that would suggest habituation to the MIS procedure. This apparent lack of habituation may be a function of the lengthy time periods between tests: my preliminary lab work indicated that certain individuals did habituate when tested repeatedly on the same day.

VII. THE DISTRIBUTION OF BEHAVIORAL TYPES: MULTIDIMENSIONAL CONTINGENCY TABLE ANALYSIS

The associations between age, sex, socioecological situation, and behavioral type were examined simultaneously via multidimensional contingency table analysis. While a two-dimensional contingency table can be used to test the independence of two variables, a multidimensional contingency table analysis can test a variety of models for independence and/or interactions between variables. The precise methodology of the technique is described by Goodman (1970, 1972), Fienberg (1970, 1972) and Jenkins (1975).

TABS program TMAC, based on Goodman's models, was used to analyze the contingency table shown in Table 16. Table 17 shows selected models assuming different sets of interactions. By testing a logical sequence of models (marginals fitted according to different hypotheses of interaction), I established that the four variables lacked joint independence and that the only significant interaction was between socioecological situation, G, and MIS type, T. Confirmation that GT is the simplest possible model which adequately explains the data should be provided by testing the significance of the differences between this model and the more complex models from which it can be derived. This check is feasible because the log-likelihood ratio corresponding to the difference between two models is distributed approximately as chi-square (Jenkins, 1975). Table 18 indicates that both GT*S and GT fit the observed

Table 16. Four way contingency table showing MIS type as a function of age, sex, and socioecological situation.

		Sociable	Avoider	Conflict
Adult Males	Shrub	1	3	6
	Colony	11	1	3
	Satellite	1	3	2
Juvenile Males	Shrub	2	1	6
	Colony	8	1	1
	Satellite	1	5	4
Adult Females	Shrub	5	6	5
	Colony	11	3	8
	Satellite	1	6	7
Juvenile Females	Shrub	5	3	3
	Colony	8	5	5
	Satellite	4	5	5

Table 17. Selected models assuming various sets of interactions among the four variables tested against the observed data. A=Age S=Sex G=Socioecological Situation T=MIS Type

Model	Log-Likelihood Ratio	df	Model Fits Data
GAS*GAT*AST*GST	3.826	4	+
GA*GS*GT*AS*AT*ST	22.695	16	+
G*A*S*T	51-376	29	-
GA*GS*GT*AS*AT	22.904	18	+
GA*GS*GT*AS*ST	23.194	18	+
GA*GS*GT*AT*ST	22.855	17	+
GA*GS*AT*AS*ST	48.993	20	-
GA*GT*AT*AS*ST	22.935	18	+
GS*GT*AT*AS*ST	24.719	18	+
GT*GA	31.791	24	+
GT*GS	25.984	24	+
GT*AS	25.298	24	+
GT*AT	33.284	24	+
GT*ST	25.983	24	+
GT*A	33.409	26	+
GT*S	26.219	26	+
GT	34.190	27	+
G	72.263	33	-
T	65.151	33	-

\+ Model fits data at 0.05 level.

\- Model does not fit data at 0.05 level.

data at the 5% level, but that the difference between the two models is significant. Unfortunately, the theory behind multidimensional contingency table analysis provides no clear way of interpreting such results (Jenkins, 1975). In the interest of parsimony, the simpler model will be presumed the more appropriate.

If MIS is a reliable indicator of an individual's response to conspecifics, then one might predict that Sociable animals would be most likely to live in colonies, whereas Avoiders would be most likely to live in satellite situations. Examination of the frequencies of MIS types in the different socioecological situations suggests that at least the first prediction holds true (Table 19). As anticipated by multidimensional contingency analysis, there was a significant relationship between MIS type and socioecological situation (Contingency Chi-Square=25.47, 4df, p=0.00004). The major source of significance was the greater than expected proportion of Sociable squirrels living in colonies. Other deviations from the expected proportions were also noteworthy. The proportion of Conflict types was higher than expected in both satellite and shrub situations and considerably lower than expected in colonies. Avoider types, however, were fairly evenly distributed among the three situations and the proportion living as satellites was actually lower than expected (rather than higher as predicted).

Svendsen (1974) reported that Social females tended to

Table 18. Partitioning of likelihood ratio chi-square statistic: differences between tested models.

Model	G	df	Model Fits Data	Difference Significant
GA*GS*GT*AS*AT*ST	22.695	16	+	
Difference: GT	26.298	4		++
GA*GS*AT*AS*ST	48.993	20	-	
GT*S	26.218	26	+	
Difference: S	7.972	1		++
GT	34.190	27	+	
Difference: T	38.075	6		++
G	72.265	33	-	
GT	34.190	27	+	
Difference: G	30.961	6		++
T	65.151	33	-	

\+ Model fits data at 0.05 level.
\- Model does not fit data at 0.05 level.
++ Difference between models significant at p=0.05.

Table 19. Two way contingency table comparing MIS type and socioecological situation.

(Expected frequencies in parentheses)

Socioecological Situation	MIS Type: Sociable	Avoider	Conflict
Shrub	10 (15.4)	10 (10.1)	26 (20.5)
Colony	36 (21.8)	10 (14.3)	19 (28.9)
Satellite	6 (14.7)	14 (19.6)	24 (19.6)

Contingency Chi-Square = 25.47; probability = 0.00004
Log-likelihood Chi-Square = 25.94; probability = 0.00003

live in cclonies, that Avoider females tended to live as satellites, and that Aggressive females usually lived as satellites or members of small harems. He also suggested that colonial resident males were typically Aggressive types, whereas male transients and satellite residents were usually Avoiders. Social type male marmots were apparently uncommon. My analysis indicated no significant interaction between either sex or age and MIS type; sex and age classes were therefore combined for analysis of distribution patterns. My data also dealt only with animals which were presumed residents. In spite of these differences, both studies demonstated that particular behavioral types are more likely to occur in certain conditions. Svendsen reported a ratio of Social to Aggressive to Avoider types of 3:3:1 in colonies and 1:4:1 at satellite sites. In ground squirrels, the observed ratios of Sociable to Conflict to Avoider types were approximately 3.5:2:1 for colonies, 1:4:2 for satellite sites, and 1:2.5:1 for shrub sites.

VIII. FIELD OBSERVATIONS OF MIS TYPES

The analysis of MIS data revealed three basic behavioral types among Columbian ground squirrels. The next step is to determine whether or not these behavioral types are distinguishable in the field. Svendsen and Armitage (1973) suggested that MIS-derived profiles "fit well" with their field observations of marmot social behavior and activity patterns, but presented only descriptive evidence. Svendsen (1974) later reported significant differences between types in reproductive characteristics, but did not specifically compare social behaviors or activity patterns between types.

Since MIS presumably simulates a social encounter, MIS types should be most readily distinguishable by their social behavior. Social behavior patterns within an established colony, however, are not equivalent to MIS encounters with previously unseen animals in a strange environment. Behavioral types might also be distinguishable on the basis of activity patterns and other nonsocial aspects of squirrel life. Svendsen and Armitage (1973), for instance, found that Avoider type marmots were characterized by unstable home ranges and high frequencies of "alert behaviors."

Classification procedures grouped the fifteen animals observed in the field into four Sociable, six Avoider, and five Conflict individuals. The uneven distribution of behavioral types suggested by the previous multidimensional contingency table analysis was also evident in the core group (Table 20): four out of five Conflict types were also

Table 20. Breakdown of core group animals by MIS type and socioecological situation.

Socioecological Situation	MIS Type		
	Sociable	Avoider	Conflict
Colony	4	5	1
Satellite	0	1	4

satellite residents. Comparisons of social interactions between adults were thus restricted to the nine Sociable and Avoider squirrels that were also colonial. Activity data and data on juvenile interactions with focal animals, however, were compared between all three types.

Field variables were in the form of hourly rates, minutes per hour, and proportions. For a given variable, the data consisted of the average value from each sampling period or eight values per individual. The limited number of individuals made a multivariate approach to the analysis of field observations impractical and necessitated a univariate approach. The data did not satisfy assumptions for a parametric analysis of variance, so were analyzed using a Hodges-Lehmann test for aligned observations (Marascuilo and McSweeney, 1977). The observations were aligned on the block medians and behavioral type and sampling period were alternately treated as blocking variables. If the null hypothesis of no differences between behavioral types was rejected, then post-hoc procedures were used to locate the source of the difference between types. Similarly, if the null hypothesis of no difference between sample periods was rejected, post-hoc procedures were used to determine which sampling periods were significantly different. Table 21 summarizes the results of the Hodges-Lehmann analysis.

Differences Between Sampling Periods

The null hypothesis of no differences between sampling

Table 21. Field observations: results of Hodges-Lehman tests for differences between MIS types and sample periods. Mean ranks which were not significantly different in pairwise comparisons are underlined at the same level. Contrast codes are arranged in the order of the mean ranks, from lowest to highest. S=Sociable A=Avoider C=Conflict

Behavior Code	MIS Types W	MIS Types Contrast	Sample Periods W	Sample Periods Contrast
G	6.939*	none	3.231	
R	44.619*	A S C	18.186*	none
L	12.223*	C S A	6.856	
N	7.473*	S A C	6.874	
CH	3.257		3.480	
A	1.366		4.050	
E	1.705		3.731	
ST	25.604*	S A C	3.048	
D	7.649*	S A C	7.635	
P	0.007		2.996	
FT	3.510		32.779*	1 2 3 4 5 6 7 8
FE	4.935		5.647	

* significant at p=0.05 or less.

Table 21. Continued

Behavior Code	MIS Types W	MIS Types Contrast	Sample Periods W	Sample Periods Contrast
ST	0.391		13.328	
Sam	6.891*	A S	5.885	
Sag	9.016*	A S	3.411	
Sav	13.621*	S A	1.560	
Sin	2.282		0.723	
CHR	5.852*	A S	2.613	
SJ	7.183*	S A C	10.404*	none
SJag	7.695*	C S A	12.725*	1 2 3 4 5

* Significant at p=0.05 or less.

periods was rejected for four variables: Resting, Total Feeding, Rate of Interaction with Juveniles, and Agonistic Interactions with Juveniles. Values for Resting, Total Feeding, and Agonistic Interactions with Juveniles increased over the season, whereas values for Rate of Interaction with Juveniles decreased over the season. The latter could reflect variable numbers of juveniles over the season since no attempt was made to correct for changes in interaction rate as a function of population density. Significant pairwise contrasts, however, were found only for Total Feeding and Agonistic Interactions with Juveniles.

These changes over time were consistent with my impression that Columbian ground squirrels tended to spend increasing amounts of time eating and resting and decreasing amounts of time interacting as the time to hibernate approached. The increased proportion of agonistic interactions with juveniles seemed to reflect a decreasing tolerance of juvenile play activity rather than active attempts to drive juveniles away. Most of the agonistic interactions with juveniles occurred when they attempted to solicit play from adult females or when their play "chases" interfered with an adult female's activities.

Differences Between Behavioral Types

The null hypothesis of no differences between types was rejected for 12 field variables: Grooming, Resting, Locomotion, Nest-Gathering, Sitting, Digging, Amicable

Interactions with Adults, Agonistic Interactions with Adults, Avoidance Interactions with Adults, Chaser, Rate of Interaction with Juveniles, and Agonistic Interactions with Juveniles. Significant pairwise contrasts between behavioral types were found for all of the above except Grooming (Table 21). For those activity variables where all three types were compared, the significant contrast always occurred between the Conflicts and either the Sociables or Avoiders: Sociable and Avoider types were not significantly different. Interpretation of this pattern is complicated by the fact that the Conflict animals were predominantly satellite residents, while the Sociables and Avoiders were predominantly colony residents. Animals living at satellite sites were not occupied with social interactions with other adults, territorial defense, or other activities associated with group-living. Satellite residents would, therefore, be expected to spend a greater proportion of their time in nonsocial activities than colonial residents. This expectation was met for all significant contrasts except Locomotion.

Sociable and Avoider squirrels were also not distinguishable on the basis of interactions with juveniles. Once again, the significant contrasts occurred between the Conflict type and one of the other two behavioral types. Conflict animals had a significantly higher rate of interaction with juveniles than Sociables and a significantly lower proportion of agonistic interactions

with juveniles than Avoiders. The interpretation of these results is also complicated by the fact that most Conflict animals lived as satellites. Satellite females interacted exclusively with their own offspring, whereas colonial females interacted with other juveniles as well. The observed differences may thus reflect differential interactions with kin and nonkin, rather than real differences between behavioral types. They may also reflect differential behavior by juveniles. The behavior of satellite juveniles appeared to differ from that of their colonial counterparts in several ways. Satellite juveniles were less active, maintained closer physical proximity to the mother, and played less than colonial juveniles. Since quantitative data were not collected on juvenile behaviors other than interactions with focal animals, it remains to be seen whether or not these apparent differences are real.

Sociable and Avoider types were significantly different in terms of social interactions with other adults, categories where the Conflict animals were not included in the comparison. The direction of these contrasts was consistent with the behavior of the two types during MIS: Sociables had a higher proportion of amicable behaviors than Avoiders, while Avoiders had a higher proportion of avoidance behaviors than Sociables. Sociable animals also had higher proportions of agonistic behaviors and acted as chasers more often than Avoiders.

Significant differences between types were found in

spite of very small sample sizes and a high degree of individual variability on most variables. Larger sample sizes might reveal further differences between types - perhaps, revealing significant differences between Sociable and Avoider individuals for nonsocial activities. To adequately test for such differences, one should ideally collect observations for greater numbers of each behavioral type from each socioecological situation. Such data would allow one to detect differences between types within a given socioecological situation, whereas the data from the present study were not always sufficient to differentiate between differences due to behavioral type and those due to socioecological situation.

Home Range Size and Percent Overlap of Home Range

Each observation area was divided into 10 x 10 meter squares for home range calculations: an animal observed in 40 squares would thus have an observed home range of 4000 square meters (Murie and Harris, 1978). A Kruskal-Wallis one way analysis of variance comparing home range sizes of the three MIS types was not significant. The percent overlap of home ranges was also calculated for the colonial animals: a Kruskal-Wallis anova comparing the percent overlap of Sociable and Avoider type home ranges was also not significant. The different behavioral types were thus not distinguishable on the basis of home range parameters.

MIS Types Within Litters

I exposed the litters from 13 satellite females to MIS and classified them using the previously mentioned SPSS discriminant analysis option for the classification of new cases. There appeared to be no tendency for juveniles to be of the same MIS type as the mother (Table 22). All three MIS types were, in fact, usually represented within a litter. Svendsen (1974) reported a comparable situation in marmots.

Table 22. Behavioral types of satellite litters.

	Juvenile MIS Type		
Mother's MIS Type	Sociable	Avoider	Conflict
Conflict	1	2	1
Conflict	2	1	2
Conflict	1	1	2
Conflict	1	1	2
Conflict	1	1	1
Conflict	1	2	1
Conflict	1	1	1
Conflict	1	2	1
Avoider	2	1	1
Avoider	1	2	0
Avoider	1	0	2
Avoider	1	0	1
Sociable	1	2	2
Total	15	16	17

IX. DISCUSSION

I have attempted to describe and evaluate the use of MIS as a behavioral profiling technique for Columbian ground squirrels. My investigation provides some, albeit limited, answers to the questions originally posed. These answers may be summarized as follows:

1. Mirror exposure elicited a set of behavioral responses that were significantly different from those observed in the same apparatus with the mirror covered.
2. MIS-derived profiles could be reduced by multivariate classification techniques to three behavioral types characterized by sociable, avoidance, and conflict responses.
3. Changes of type upon retesting were rare.
4. The proportions of the three MIS types did not differ significantly between sex and age classes, but did vary with socioecological situation.
5. The different behavioral types differed for several measures of activity and social interaction collected in the field.

That behaviors after mirror exposure differed from those before came as no surprise. Nevertheless, the recording of behaviors before mirror exposure provided a desirable control which has often been neglected in MIS studies. The behaviors observed during this period could themselves be used as the basis for behavioral classification since the arena environment alone was

sufficient to induce differential behavior patterns. Such a classification, however, would probably reflect differences in general activity rather than sociality.

Ground squirrel responses to MIS were consistent with the contention that a mirror-image is viewed as an unfamiliar conspecific (Gallup, 1975) and were similar to those reported for other vertebrate species (Gallup, 1968), particularly marmots (Svendsen and Armitage, 1973). Aggressive displays, however, were infrequent, whereas they are the most common response to MIS in many other species (Gallup, 1968). Multivariate classification procedures partitioned the test animals into three statistically distinct "types" which I labeled "Sociable", "Avoider", and "Conflict". While the Sociable and Avoider types were readily interpretable in terms of sociality, the Conflict group was somewhat of an enigma since it included animals with diverse behavior patterns whose only common trait seemed to be their failure to either interact with or retreat from the mirror. They are perhaps best described as "curious, but cautious".

Changes of type upon retesting were rare, but more work would be needed to determine the extent of this consistency between years. Major biological events such as the birth and emergence of juveniles had no apparent effect on the behavioral type of retested ground squirrels. This suggests that whatever MIS measures is relatively stable and probably unaffected by changes in hormone levels or season. MIS type

might, however, change with age or changes in health or social status. The proportions of MIS types did not differ significantly between juveniles and adult age classes, but individuals could conceivably change type as they aged. The few recorded changes of type were not accompanied by any noticeable changes in health or social status.

MIS thus provides a consistent technique for establishing behavioral types in ground squirrels. These types, however, could represent mere testing artifacts with little or no biological significance. My results suggest that this is nct the case, but also suggest that determining the role of these types in ground squirrel social systems will require far more extensive research. The meaning of these experimentally-derived groups depends on what MIS actually measures. It is doubtful that a single behavioral index such as MIS could adequately measure all aspects of a behavioral phenotype or "personality"; at best, MIS may measure certain limited dimensions of behavioral phenotypes. The nature of the observed behaviors suggested that MIS may measure some aspect of social confidence or "boldness". Svendsen and Armitage (1973) assumed that whatever MIS measured was relevant to social structure and population dynamics. At this point, it is perhaps safer to assume only that MIS type may measure certain dimensions of behavioral phenotypes which <u>may</u> be important in determining how individuals function within their social milieu.

Evidence that MIS types might be something more than

irrelevant artifacts came from field observations of distribution and behavior. Like Svendsen and Armitage (1973), I found that MIS types "fit well" with field observations of behavior. Significant differences between types were found for a number of variables representing both general activity and social interaction data. The nature of the animals observed, however, made it difficult to determine whether these differences were a function of behavioral type or socioecological situation. As noted earlier, the two factors are apparently interrelated and determining their relative influence will require more extensive research designed to do so.

In spite of these complications, the fact that so many significant differences between types were found suggests that there is a relationship between behaviors observed during MIS and those observed in the field. This relationship was by no means obvious; my subjective impressions of individual squirrel "personalities" in the field were sometimes quite at odds with MIS "type". Moreover, one might not expect to detect such differences from observations of routine behaviors of established residents whose behavior patterns have presumably already been influenced by previous experiences and social encounters.

Perhaps the strongest argument for the biological significance of MIS types is provided by their differential distribution. While no one behavioral type was exclusive to

any one socioecological situation, certain types were more likely to occur in particular situations. Sociable squirrels were most heavily concentrated in colonies, while conflict animals tended to live in either shrub or satellite situations. Avoider squirrels were relatively evenly distributed. These observations raise the difficult problem of distinguishing between cause and effect. It may be, as Svendsen (1974) suggested, that different behavioral types are best suited to, and most likely to maximize their fitness in, particular socioecological conditions. Or certain conditions could be suboptimal for all behavioral types, intraspecific aggression could force subordinates to disperse to these suboptimal areas and certain types could be subordinate more frequently than others. To clarify the relationship between behavioral types and socioecological situation we should know:

1. the relative importance of genotypic and phenotypic influences in determining which individuals belong to which type,
2. if dominance is correlated with type,
3. if certain socioecological situations can be considered suboptimal,
4. how individuals end up where they do -e.g. whether dispersal is a response to social pressure or to some innate drive, and
5. if the fitness of the different behavioral types varies with socioecological situation.

Assessing the relative contributions of genetic and environmental/experiential factors to behavioral type is impossible at this point. The apparent stability of type, for instance, could be explained either by some degree of genetic control or by the influence of early experience. In the few cases where offspring of known type mothers were tested, there was no tendency for the offspring to be of the same type as the mother. All three types were, in fact, usually represented within the same litter. This parallels the findings for marmots (Svendsen,1974), but in both studies sample sizes were very small and the father's type was not known, hence no reliable conclusions could be drawn. Resolving the nature-nurture problem would require estimates of the heritability of type: these might be obtained by combining testing of known kin (at different ages) with electrophoretic procedures.

Field observations of social behavior suggested that MIS type may be correlated with dominance. Sociable females had higher proportions of amicable, agonistic, and chasing behaviors than Avoiders, while Avoiders tended to avoid interactions more often than Sociables. Sociable animals thus appeared more "socially confident" than Avoiders and it seems likely that this "confidence" would be reflected in dominance relations. It is more difficult to assess how Conflict individuals fit into this interpretation of dominance. Since Conflict animals were the most aggressive during MIS, it is possible that they might be dominant to

Sociable types, but the Conflict individuals observed were satellites and had little opportunity to interact with other adults. It is also possible that behavioral type is but one of many factors (such as age and the location of interactions) which determine dominance. Nevertheless, paired encounters between different type individuals could help determine whether a correlation between dominance and behavioral type exists.

Determining whether or not certain socioecological situations are "suboptimal" would require both extensive habitat assessment and comparative survival data. Open colonial and satellite sites appeared comparable in terms of vegetative composition and cover, but no quantitative comparisons were made. Shrub-dwelling squirrels were rarely observed feeding in adjacent open meadows and presumably relied on food sources within the shrubs. Comparisons of food availability and nutrient quality should therefore be made before ruling out food as a factor associated with the suitability of the different situations. Other factors which might influence a situation's suitability include the supply of burrow and hibernacula sites and snow depth.

The most obvious differences between the three socioecological situations, e.g. population density and degree of cover, are also the hardest to evaluate. Satellite animals lived in comparative isolation, whereas colony and shrub residents lived in close proximity to other squirrels, but under different conditions of visibility. Group- living

may provide advantages such as protection from predation, but also disadvantages such as competition for food and other resources. Moreover, the relative benefits of group-living as compared to isolation may depend upon the individual's behavioral type (Svendsen, 1974). To further complicate the picture, population density may be related to the degree of cover, and social systems in shrub habitats may be quite different from those in open colonies.

Shrub and open situations differ greatly in their relative visibility and potential for visual communication. Since ground squirrels appear to rely heavily on vision to detect both predators (Adams, 1966) and conspecific intruders (Murie and Harris, 1978), the degree of visibility in a socioecological situation could be an important determinant of its "quality". Reduced visibility could, for example, reduce the likelihood of ground squirrels detecting predators (Adams, 1966; Dunford, 1977) or vice versa. It could also create an "ecological cutoff" effect similar to that described by Melchior (1965) as the "cessation of an interspecific or intraspecific interaction between two or more individuals by an inanimate environmental feature." Such an effect might lead to fewer chases and less rigorous territorial defense than occur in open areas (Murie and Harris, 1978). Restricted opportunities for visual detection could thus act to reduce territory size and defense, thereby allowing higher densities in shrub situations than in open colonies. Density and visibility are obviously important

factors in determining a site's "quality", but only if we can demonstrate that survival differs as a function of these factors would we be justified in labeling a particular condition as "suboptimal".

Even if we did feel safe in labeling certain socioecological situations as "suboptimal", we would still have to explain how individuals end up in those situations. That, however, would require a far greater understanding of the underlying mechanisms of dispersal than we now have - as well as an understanding of habitat and social "preferences". We would also need to distinguish between residents which were born in suboptimal situations and those which moved there later, since the advantages of familiarity coupled with the risk of dispersing to an untested environment might outweigh any disadvantages of the natal environment. A further distinction would need to be made between voluntary and aggression-induced dispersal, since an animal could disperse voluntarily, but be unable to find unoccupied territory in the preferred situation. Finally, we should recognize that there may be no such thing as a single optimal or preferred situation. An animal's "preferred" socioecological situation may be determined by multiple factors including genotype, behavioral type, past experiences and interactions with conspecifics. Within certain physical limits, there may be a wide range of suitable situations.

Anecdotal evidence suggests that dispersal in Columbian

ground squirrels probably occurs in the yearling age class, but we know little about the factors which cause particular individuals to disperse. Evidence from other rodent species indicates that both genetic and behavioral differences may exist between dispersers and nondispersers (Krebs et al., 1976; Myers and Krebs, 1974; Fairbairn, 1978). It is conceivable that the behavioral differences revealed by MIS could be related to genetic differences between dispersing and nondispersing individuals. However, the mere existence of genetic and behavioral differences between dispersers and nondispersers does not mean that these differences are causally related to dispersal. It is clearly essential to know the behavioral antecedants of dispersal at the level of the individual. MIS coupled with a knowledge of individual experiential histories and genotypes could increase our understanding of dispersal.

While an explanation for dispersal should provide satisfaction enough for any biologist, we should go one step further and compare the "fitness" of each behavioral type in different socioecological situations. I was unable to evaluate fitness because of problems in determining kinship within colonies. Svendsen (1974), however, reported that the three behavioral types differed greatly in the proportion of young they contributed to the population and implied that their fitness was a function of social situation. A parallel situation conceivably could exist in ground squirrels. If we could demonstrate that the fitness of behavioral types does,

in fact, differ between socioecological situations and if we could demonstrate a genetic basis for type, then we would be justified in considering the possibility of a genetically based polymorphism. Until that time, however, it seems safest to avoid the temptation of evolutionary speculations about behavioral types and concentrate on obtaining the data necessary to shed light on such speculation.

With so many critical questions yet to be answered, MIS may seem of dubious value at this time. Given the complex, multifactorial nature of behavior, it seems unlikely that MIS could be used to predict the behavior of individual ground squirrels in the field. What MIS can do, however, is identify some fundamental behavioral differences which may provide some insight into larger problems of social organization and population dynamics. The differential distribution of behavioral types, for instance, suggests that the technique might be particularly valuable as an adjunct to dispersal studies, but it could also be useful for studies dealing with dominance or the development of behavior. Perhaps the most pressing need now is for a long-term study which would follow individuals of known type from emergence as juveniles through reproductive age and maturity and attempt to answer some of the many questions raised by this preliminary investigation.

Literature Cited

Adams, G.D. 1966. Ecology of the Columbian ground squirrel in the Sheep river region. Unpublished M.Sc. Thesis. University of Alberta, Edmonton, Alberta. 120 pp.

Altman, J. 1974. Observational study of behavior: Sampling methods. Behaviour 48:227-267.

Anderberg, M.R. 1973. Cluster Analysis for Applications. Academic Press. New York.

Armitage, K.B. 1975. Social behavior and population dynamics of marmots. Oikos 26:341-354.

Aspey, W.P. 1977. Wolf spider sociobiology: I. Agonistic display and dominance-subordinance relations in adult male Schizocosa crassipes. Behavior 62:103-141.

_____, and J.E. Blankenship. 1977. Spiders and snails and statistical tales: Applications of multivariate analyses to diverse ethological data. In B.A. Hazlett (ed.). Quantitative Methods in the Study of Animal Behavior. Academic Press. New York. pp.75-120.

Balph, D.F. and A.W. Stokes. 1963. On the ethology of a population of Uinta ground squirrels. Amer. Midl. Natur. 69:106-126.

Bekoff, M. 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. Amer. Natur. 3:715-732.

Betts, B.J. 1976. Behavior in a population of Columbian ground squirrels, Spermophilus columbianus columbianus. Anim. Behav. 24:652-680.

Comrey, A.L. 1973. A First Course in Factor Analysis. Academic Press. New York.

Cormack, R,M. 1971. A review of classification. J. Roy. Statist. Soc. (A) 134:321-353.

Davies, W.G. 1978. Cluster analysis applied to the classification of postures in the Chilean flamingo. Anim. Behav. 26:381-388.

Dumas, F.M. 1949. The coefficient of profile similarity. J. Clin. Psychol. 5:123-131.

Dunford, C. 1977. Social system of round-tailed ground

squirrels. Anim. Behav. 25:885-906.

_____. 1977. Behavioral limitation of round-tailed ground squirrel density. Ecology 58:1254-1268.

Fairbairn, D.J. 1978. Behavior of dispersing deer mice (Peromyscus maniculatus). Behav. Ecol. Sociobiol. 3:265-282.

Fienberg, S.E. 1970. The analysis of multidimensional contingency tables. Ecology 51:419-435.

_____. 1972b. The analysis of incomplete multidimensional contingency tables. Biometrics 28:177-202.

Fox, M.W. 1975. Evolution of social behavior in canids. In M.W. Fox (ed.). The Wild Canids. Van Nostrand Reinhold. New York. pp.429-460.

Gallup, G.G. 1968. Mirror-image stimulation. Psychol. Bull. 70:782-793.

_____. 1975. Towards an operational definition of self-awareness. In R.H. Tuttle (ed.). Socioecology and Psycholcgy of Primates. Mouton Publ. The Hague. pp. 309-342.

Goodman, L.A. 1970. The multivariate analysis of qualitative data: Interactions among multiple classifications. J. Amer. Stat. Assoc. 65:226-256.

_____. 1972. A general model for the analysis of surveys. Amer. J. Sociol. 77:1035-1086.

Gorsuch, R.L. 1974. Factor Analysis. W.B. Saunders Co. Toronto.

Harris, R.J. 1975. A Primer of Multivariate Statistics. Academic Press, New York.

Ito, K. 1969. On the effects of heteroscedasticity and nonnormality upon some multivariate test procedures. In P.R. Krishnaiah (ed.). Multivariate Analysis-II. Academic Press. New York. pp.87-120.

_____, and W.J. Schull. 1964. On the robustness of the T^2 test in multivariate analysis of variance when variance:ccvariance matrices are not equal. Biometrika 51:71-82.

Jacobs, G.H. 1978. Spectral sensitivity and color vision in the grcund-dwelling sciurids: Results from Golden-Mantled ground squirrels and comparisons for 5 species. Anim. Behav. 26:409-421.

Jenkins, S.H. 1975. Food selection of beavers: a multidimensional contingency table analysis. Oecologia (Berl.) 21:157-173.

Krebs, C.J. 1970. Microtus population biology: behavioral changes associated with the population cycle in M. ochrogaster and M. pennsylvanicus. Ecology 51:34-52.

_____, J. Wingate, J. Leduc, J.A. Redfield, M. Taitt, and R. Hillborn. 1976. Microtus population biology: Dispersal in fluctuating populations of M. townsendii. Can. J. Zool. 34:79-93.

Lott, D.F. and P.N. Brody. 1966. Support of ovulation in the ring dove by auditory and visual stimuli. J. Comp. Physiol. Psychol. 62:311-313.

Marascuilo, L.A. and M. McSweeney. 1977. Nonparametric and Distribution-Free Methods for the Social Sciences. Brooks/Cole Publ. Monterey, California.

Maurus, M. and H. Pruscha. 1973. Classification of social signals in squirrel monkeys by means of cluster analysis. Behavior 47:106-190.

Melchior, H.R. 1965. Ecological cutoff as a possible determinate of Arctic ground squirrel population densities. Bull. Ecol. Soc. Amer. 46:104.

Michael, C.R. 1968. Receptive fields of single optic nerve fibers in a mammal with all-cone retina. J. Neurophysiol. 31:249-282.

_____. 1972. Visual receptive fields of single neurons in the superior colliculus of the ground squirrel. J. Neurophysiol. 35:815-832.

_____. 1973. Opponent-color and opponent-contrasting cells in the lateral geniculate nucleus of the ground squirrel. J. Neurophysiol. 36:536-550.

Morgan, B.J.T., M.J.A.Simpson, J.P.Hanby and J. Hall-Craggs. 1975. Visualizing interaction and sequential data in animal behavior: Theory and application of cluster-analysis methods. Behavior 56:1-43.

Murie, J.O. and M.A.Harris. 1978. Territoriality and dominance in male Columbian ground squirrels (Spermophilus columbianus). Can. Jour. Zool. 56:2402-2412.

Myers, J.H. and C.J. Krebs. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles Microtus pennsylvanicus and Microtus ochrogaster. Ecol.

Monogr. 41:53-78.

Overall, J.E. and C.J.Klett. 1972. Applied Multivariate Analysis. McGraw-Hill. New York.

Pimentel, R.A. and D.F. Frey. 1978. Multivariate analysis of variance and discriminant analysis. In P.W. Colgan (ed.). Quantitative Ethology. John Wiley & Sons. Toronto.

Puri, M.L. and P.K.Sen. 1971. Nonparametric methods in multivariate analysis. Wiley. New York.

Ritter, W.E. and S. Benson. 1934. "Is the poor bird demented?" Another case of "shadow boxing". Auk 51:169-179.

Schusterman, R.J., R. Gentry, J.Schmook. 1966. Underwater vocalizations of sea lions: social and mirror stimuli. Science 154:540-542.

Sherman, P.W. 1977. Nepotism and the evolution of alarm calls. Science 197:1246-1253.

Steiner, A.L. 1970a. Etude descriptive de quelques activités et comportements de base de Spermophilus columbianus (Ord). I. Locomotion, soins du corps, alimentation, fouissage, curiosité et alarme, reproduction. Rev. Comp. Anim. 4:3-21.

_____. 1970b. Etude descriptive de quelques activités et comportements de base de Spermophilus columbianus (Ord). II. Vie de groupe. Rev. Comp. Anim. 4:23-42.

_____. 1971. Play activity of Columbian ground squirrels. Z.Tierpsychol. 28:247-261.

_____. 1972. Mortality resulting from intraspecific fighting in some ground squirrel populations. J.Mammal. 53:601-603.

_____. 1973. Self- and allogrooming behavior in some ground squirrels (Sciuridae), a descriptive study. Can. J. Zool. 51:151-161.

_____. 1974. Body-rubbing, marking, and other scent-related behavior in some ground squirrels (Sciuridae), a descriptive study. Can J. Zool. 52:889-906.

_____. 1975. "Greeting" behavior in some Sciuridae, from an ontogenetic, evolutionary, and socio-behavioral perspective. Naturaliste. Can. 102:737-751.

Svendsen, G.E. 1974. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. Ecology 55:760-776.

_____, and K.B.Armitage. 1973. Mirror-image stimulation applied to field behavioral studies. Ecology 54:623-627.

Tigges, J. 1970. Retinal projections in the subcortical optic nuclei in diurnal and nocturnal squirrels. Brain Behav. Evol. 3:121-134.

Tolman, C.W. 1965. Feeding behavior of domestic chicks in the presence of their own mirror-images. Can. Psychol. 6:227.

Vaidya, P.G. 1964. The retina and optic nerve of the ground squirrel Citellus tridecemlineatus tridecemlineatus J. Comp. Neurol. 122:347-354.

West, R.W. and J.E.Dowling. 1975. Anatomical evidence for cone and rod-like receptors in the gray squirrel, ground squirrel, and prairie dog. J. Comp. Neurol. 159:439-460.

Wishart, D. 1975. Clustan C User Manual. Computer Center, University College, London.

Appendix 1

Linear Typal Analysis: Pure-Type Profiles Computed as Means of Profiles for Individuals Most Highly Related to Each Pure Type.

Behavior	Pure-Type 1	Pure-Type 2	Pure-Type 3
Chirp	0.84	4.66	2.25
Alarm Call	0.53	1.69	2.97
Tooth Chatter	0.19	0.00	1.88
Sit	4.31	1.66	3.57
Stand	0.49	0.55	2.78
Alert Position	5.20	0.59	3.55
Lying/Crouch	0.79	11.52	2.45
Explore	2.23	0.14	0.40
Tail Flare	4.97	10.24	12.12
Tail Flick	0.56	0.47	3.52
Motionless	2.44	13.09	6.50
Groom	2.64	0.24	0.13
Sniff/Scratch	5.09	0.19	1.08
Bipedal Walk	1.00	0.03	0.17
Touch Mirror	3.37	0.00	0.23
Front 1/3	11.14	0.90	4.73
Middle 1/3	0.90	1.16	4.68
Rear 1/3	0.50	4.21	4.18
Rear Corners	0.00	8.59	0.52
Entire Arena	1.71	0.14	0.58
Time to approach	2.60	0.98	5.35
Nose	9.17	0.22	1.72
Paw/Muzzle	7.20	0.00	0.43
Parallel Walk	7.94	0.19	1.22
Approach/Withdraw	0.30	0.29	1.57
Lunge	0.43	0.00	1.42
Orient Towards	12.06	8.64	13.40
Orient Parallel	9.37	3.02	2.20
Orient Away	1.43	3.48	0.45
Rapid Retreat	0.04	0.16	0.52

Pure-Type 1 = "Sociable"
Pure-Type 2 = "Avoider"
Pure-Type 3 = "Conflict"

Appendix 2a

Cluster One: Cluster Diagnosis of Means, Standard Deviations, F-Ratios and T-Values.

Behavior	F-Ratio	T	MN	STD
Chirp	1.051	0.168	2.792	3.411
Alarm Call	1.328	0.538	2.953	2.765
Tooth Chatter	1.990	0.455	1.698	2.761
Sit	0.711	0.011	3.660	2.868
Stand	1.836	0.522	2.255	2.999
Alert Position	0.588	-0.072	3.085	2.815
Lying/Crouch	0.415	-0.232	3.623	3.666
Explore	0.385	-0.270	0.566	1.024
Tail Flare	0.507	0.549	12.207	4.667
Tail Flick	1.423	0.605	3.264	3.193
Motionless	0.418	-0.043	7.217	3.335
Groom	0.250	-0.459	0.358	0.928
Sniff/Scratch	0.246	-0.380	1.104	1.366
Jump	0.000	-0.380	0.000	0.000
Bipedal Walk	0.217	-0.266	0.189	0.536
Touch Mirror	0.311	-0.359	0.453	1.281
Front 1/3	0.581	-0.234	4.840	4.308
Middle 1/3	1.206	0.541	4.066	3.972
Rear 1/3	1.063	0.506	4.755	4.344
Rear Corners	0.159	-0.403	0.745	2.260
Entire Arena	0.216	-0.208	0.528	0.758
Time to Approach	1.665	0.500	4.264	4.576
Nose	0.203	-0.477	1.698	2.174
Paw/Muzzle	0.097	-0.553	0.491	1.340
Parallel Walk	0.231	-0.443	1.538	2.148
Approach/Withdraw	1.754	0.507	1.321	1.754
Lunge	0.582	0.145	1.255	1.821
Orient Towards	0.394	0.339	12.906	3.229
Orient Parallel	0.378	-0.471	3.038	3.183
Orient Away	0.182	-0.343	0.415	1.585
Rapid Retreat	1.959	0.273	0.368	0.865

Cluster 1 = "Conflict"
T-Value = (Cluster MN - Overall MN)/Overall STD

Appendix 2b

Cluster Two: Cluster Diagnosis of Means, Standard Deviations, F-Ratios, and T-Values.

	F-Ratio	T	MN	STD
Chirp	1.576	0.450	3.731	4.176
Alarm Call	0.88	-0.095	1.433	2.251
Tooth Chatter	0.280	-0.398	0.030	0.172
Sit	0.280	-0.824	0.821	1.800
Stand	0.120	-0.382	0.254	0.766
Alert Position	0.060	-0.839	0.269	0.898
Lying/Crouvh	0.353	1.436	13.104	3.376
Explore	0.032	-0.577	0.060	0.295
Tail Flare	1.182	0.083	9.149	7.125
Tail Flick	0.038	-0.565	0.134	0.519
Motionless	0.060	1.280	14.045	1.261
Groom	0.004	-0.644	0.015	0.122
Sniff/Scratch	0.019	-0.732	0.134	0.385
Jump	4.005	0.185	0.015	0.122
Bipedal Walk	0.011	-0.417	0.015	0.122
Touch Mirror	-0.000	-0.556	0.000	0.000
Front 1/3	0.079	-1.056	0.194	1.588
Middle 1/3	0.979	-0.318	0.955	3.578
Rear 1/3	1.433	0.011	2.672	5.043
Rear Corner	1.103	1.421	11.089	5.954
Entire Arena	0.065	-0.476	0.090	0.417
Time	0.035	-0.650	0.164	0.665
Nose	0.003	-0.817	0.060	0.239
Paw/Muzzle	0.000	-0.667	0.000	0.012
Parallel Walk	0.002	-0.777	0.045	0.208
Approach/Withdraw	0.189	-0.355	0.179	0.575
Lunge	2.249	-0.005	0.895	3.581
Orient Towards	1.767	-0.678	7.671	6.837
Orient Parallel	1.069	-0.562	2.567	5.352
Orient Away	2.714	0.590	3.881	6.119
Rapid Retreat	0.575	-0.081	0.149	0.469

Cluster Two = "Avoider"

Appendix 2c

Cluster Three: Cluster Diagnosis of Means, Standard Deviations, F-Ratios and T-Values.

Behavior	F-Ratio	T	Mn	STD
Chirp	0.160	-0.490	0.602	1.329
Alarm Call	0.154	-0.518	0.418	0.941
Tooth Chatter	0.239	-0.220	0.378	0.958
Sit	1.047	0.552	5.500	3.480
Stand	0.223	-0.303	0.429	1.045
Alert Position	1.184	0.652	5.745	3.996
Lying/Crouch	0.072	-0.731	0.786	1.528
Explore	1.560	0.686	2.143	2.061
Tail Flare	0.668	-0.650	4.347	5.356
Tail Flick	0.525	-0.268	0.929	1.938
Motionless	0.462	-0.829	3.163	3.507
Groom	1.105	0.911	4.663	2.939
Sniff/Scratch	1.137	0.911	4.663	2.939
Jump	0.000	-0.061	0.000	0.000
Bipedal Walk	2.013	0.572	1.153	1.633
Touch Mirror	1.495	0.769	3.041	2.806
Front 1/3	0.309	0.975	11.673	3.142
Middle 1/3	0.283	-0.368	0.775	1.924
Rear 1/3	0.066	-0.555	0.286	1.084
Rear Corner	0.000	-0.535	0.000	0.012
Entire Arena	1.995	0.550	1.765	2.305
Time	0.378	-0.092	2.163	2.181
Nose	0.682	1.075	9.184	3.983
Paw/Muzzle	0.916	1.054	7.418	4.127
Parallel Walk	0.868	1.012	8.041	4.127
Approach/Withdraw	0.294	-0.305	0.245	0.719
Lunge	0.576	-0.154	0.541	1.817
Orient Towards	0.701	0.097	11.663	4.307
Orient Parallel	0.378	0.894	10.102	3.183
Orient Away	0.369	-0.032	1.571	2.257
Rapid Retreat	0.128	-0.240	0.051	0.221

Cluster Three = "Sociable"